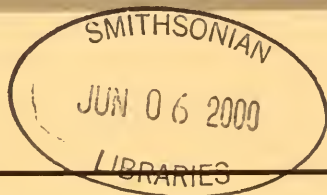




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A Study of the Bionomy of the Spanish Pollen Wasp *Ceramius hispanicus* Dusmet (Hymenoptera, Vespidae, Masarinae): Nesting, Mating, and Flower Associations

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Abstract.—Data about the bionomy of the Spanish pollen wasp species *Ceramius hispanicus* Dusmet are presented for the first time. Following the concept of Gess and Gess (1988) *C. hispanicus* can be characterized by the following ethological elements: a. Nest excavated in non-friable soil; b. Burrow surmounted by a turret from earth extracted from within the burrow; c. Nest possibly annual; d. Nest with relatively short main shaft, main shaft vertical to sub-vertical, with an expansion at the bottom of the shaft; e. Main shaft not terminated by a cell; f. Secondary shafts absent; g. Cells sub-horizontal, in a group to one side, all at different depths; h. A constructed mud-cell within an excavated-cell, formed from earth excavated within the burrow; i. Main forage plants are representatives of Cistaceae, Primulaceae, Lamiaceae, and Fabaceae. The entrance turret of the nest is unique in that it is reduced to three distally converging processes. During nest excavation the females perform pellet dropping flights and use a defined pellet-dropping area. Water is used to soften the soil. Females alight on the edge of a water source to collect water. Cell construction rate during this investigation was about 0.5 cells per day. Analysis of brood cell contents revealed *Ceramius hispanicus* to be polylectic. Cells were found to be provisioned with pollen originating from six different plant families. The most important pollen sources were *Helianthemum* (Cistaceae), *Coris* (Primulaceae), several species of Lamiaceae, and *Lotus* (Fabaceae). Pollen grains of the same plant taxa were found in crop and rectum of both male and female wasps. Males patrol and perch at water and to a lesser extent at flowers. Pairings were frequently observed at water. The daily period of activity lasted about 10 hours. Activity of males at water was high in the morning and declined during the day, while female activity increased towards the afternoon.

The genus *Ceramius* shows a disjunct distribution with six species-groups occurring in the Afrotropical Region and two species-groups in the Palaearctic (Richards 1962, Gess 1992). For the Afrotropical taxa it has been shown that there are distinct differences between the species-groups in regard to nest construction and flower association (Gess 1996, Gess and Gess 1980, 1986, 1988, 1990). By contrast, the bionomy of the Palaearctic species is insufficiently known (cf. Gess 1996) to make it possible at present to draw conclusions about the evolution of life history traits

within the whole genus. For the Palaearctic Region comprehensive information is only available for *Ceramius tuberculifer* Saussure (Ferton 1901, Giraud 1863, 1871, Mauss 1996a). The knowledge of the bionomy of the remaining 13 species is very poor (cf. Fonscolombe 1835, Mauss 1998, Richards 1963), bionomical data concerning *Ceramius hispanicus* Dusmet are completely lacking. Like *Ceramius tuberculifer*, *C. hispanicus* belongs to *Ceramius* species-group 7 of Richards (cf. Mauss 1996b). However, these species are not very closely related, i.e. *C. hispanicus* is not a mem-

ber of the *C. lusitanicus*-complex (Mauss 1996b). Biogeographically *C. hispanicus* seems to be restricted to Central, Eastern and Southern Spain (cf. Ceballos 1956: 342, Richards 1962: 107, Mauss unpubl.).

Data concerning habitat, nest architecture, flower visiting, male activity and mating of *C. hispanicus* are presented here for the first time and are compared with ethological accounts for other species of *Ceramius*.

METHODS

Investigations were carried out from 19 to 26 June 1998. Weather conditions were good throughout the whole period. Maximum air temperatures were circa 30 °C. Sunrise took place at 4h24, sun-transit at 11h56 and sunset at 19h28 (Bien in lit.). Time used is Greenwich Time. Observations were made with the aid of close-up binoculars (Eschenbach Binoskop) and documented using a 35 mm camera with a 100 mm lens (scale up to 1:1) or a 300 mm lens.

Activity of males and females at water was measured on 21 June (from 8h30 to 18h30) and 24 June (from 7h00 to 18h30). A rectangular sample area of 2m × 1m was marked out with a string. The area was completely shaded by the ridge of a mountain after 17h30. Accuracy of counting was improved by use of mechanical hand-counters. Every half hour a measuring cycle lasting 20 minutes was carried out following the sequence:

1. Activity of females measured by counting the number of females sitting on the ground of the sample area every 30 s during a period of 300 s, leading to 10 counts per period.

2. Activity of males measured by counting crossings of the string into the sample area (category "males flying") during a period of 600 s and counting landings on a perch within the sample area (category "males perching").

3. Activity of females measured again during a period of 300s as described in 1.;

female activity per half hour is the sum of the 20 counts of a complete measuring cycle (category "females at water").

Copulations were counted during the complete 1200 s of the measuring cycle irrespective whether they occurred inside or outside of the sample area. A situation was rated as a "copulatory attempt" when at least a short struggle on the ground could be observed after a male approached a female and pounced on her.

Finally, two thermometers (precision: 0.5°C) were read one of which was situated 0.5 m above the ground in the shade within a juniper tree (T_{air}), the other one was placed on the wet ground with its point in the shadow of plants (T_{ground}). Short notes were made about the weather. Radiation conditions were noted applying the categories "cloudless" (sun not covered during the whole period), "hazy" (sun covered by hazy clouds at least for a short period, resulting in half shade) and "cloudy" (sun covered by clouds at least for a short period, resulting in shade). The observed frequencies of the measured behavioural categories were summed up for every hour. Then the proportion of activity for each hour to total activity for the day was calculated separately for each category and expressed as a percentage. For statistical analysis, a Chi square test was performed which was calculated by Abacus Concepts, StatView® Student for Macintosh. For 21 June the period from 8h30 to 12h30 was compared with the period from 12h30 to 16h30. For 24 June the period from 6h30 to 12h30 was compared with the period from 12h30 to 18h30. For each category the observed frequencies were tested against the expected equal distribution.

For nest excavation on 26 June the shaft of each nest was completely filled with Maizena® (fine maize flour) which was injected with a squeezing bottle. Nests were carefully excavated afterwards. Measurements were taken by use of small strips of graph paper, orientation of the cells was

measured with a bearing-compass. All nest cells were collected and stored in a refrigerator for three days. Afterwards, all cells were measured (external maximal dimensions) using a stereo-microscope (Wild M3) with a calibrated ocular-micrometer; then they were opened and the contents were recorded.

Flowering plants in the neighbourhood of the nesting site were collected and preserved both dried and in 70% ethanol. They are named according to Tutin et al. (1964–1980). Pollen samples from the nest and the alimentary tract of imagines fixed in Bouin's solution were prepared using the method outlined by Westrich and Schmidt (1986). The different pollen types were ascertained under a light microscope at a magnification of 400× or 1000× and determined to the family or genus level with the aid of a reference collection consisting of pollen samples of 500 mainly Mediterranean plant species including those growing at the nesting site. Exact knowledge of the plant species flowering at the study site during nest provisioning in some cases allowed pollen determination down to species level. The percentage of the different pollen types per brood cell was estimated by counting 50 grains at each of 30 loci distributed randomly over the cover slip. For each gut sample between 100 and 250 pollen grains were counted.

RESULTS

Description of the habitat.—A large population of *Ceramius hispanicus* was localized in the Barranco de Zorita (GPS: 01°26.402' W 40°27.334' N), a small valley in the Sierra de Albarracín about 6 km north of Albarracín in Teruel province, situated on the north-east slope of the Vallejo Largo at an altitude of 1200 m. The narrow, steeper part of the valley was orientated from the east-south-east (downstream) to the west-north-west (upstream); at the upper end it got wider, sloped only gently and changed its direc-

tion towards the southwest. A water trough which was supplied by a perpetual spring non-seasonally was situated at the upstream end of the narrow part of the valley. The water ran away from the trough into a little stream (Fig. 1) that dried out after about 100 m. Further downstream a few puddles remained at first but they dried out during the observation period. Two small ponds were situated about 100 m upstream of the trough, the border of which was completely overgrown with rushes (*Juncus* sp., Juncaceae). The whole area was covered by sparse montane forest, on calcareous soil, dominated by trees and shrubs of different junipers (*Juniperus* sp., Cupressaceae) (cf. Polunin and Smythies 1973) forming a Junipereto hemisphaerico-thuriferae sgmentum (Rivas-Martinez 1986). The ground cover was about 70% in the valley but decreased markedly uphill where it became more rocky and much drier (Fig. 1). The following plant species were in flower: the Lamiaceae *Nepeta nepetella* L., *Marrubium supinum* L., *Sideritis spinosa* Lam. and *Thymus zygis* L., the Cistaceae *Helianthemum apenninum* (L.) Mill. and *H. cinereum* (Cav.) Pers., the Fabaceae *Lotus corniculatus* L., *Coronilla minima* L. and species of *Ononis*, *Hippocrepis*, *Onobrychis*, *Medicago* and *Vicia*, the Primulaceae *Coris monspeliensis* L., the Asteraceae *Anacylus clavatus* Pers. and *Achillea* sp., the Resedaceae *Reseda lutea* L., the Boraginaceae *Echium vulgare* L., the Rosaceae *Potentilla reptans* L. and unidentified species of Brassicaceae, Cichorioideae, Convolvulaceae and Crassulaceae. The area was grazed by sheep and goats. A small cornfield adjoined in the upper, widened part of the valley.

Nest site.—An aggregation of five nests was located on a bank of hard, clayey soil mixed with some gravel. The bank was about 20 m long, 2.5 m wide and rose above the adjacent terrace by 0.4 m. It was situated about 50 m upstream of the ponds and ran from the southwest to the

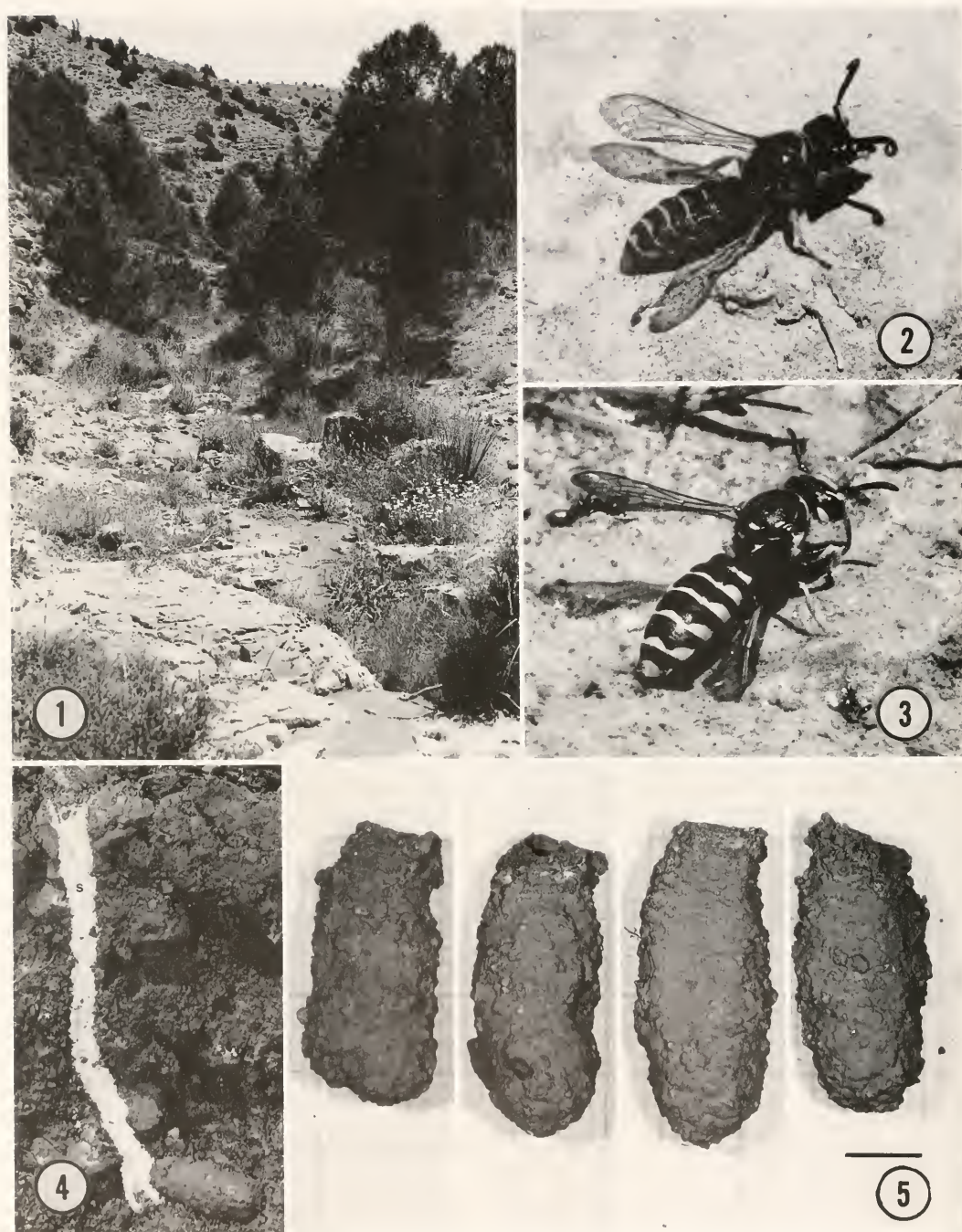


Fig. 1-5. 1, Habitat of *Ceramius hispanicus* at Barranco de Zorita (Prov. Teruel, Spain) covered by sparse montane forest dominated by different junipers. Males patrolled along the stream in the centre where females collected water. 2, Male of *Ceramius hispanicus* perching on a stone close to the water (glossa visible between slightly opened mandibles). 3, Female of *Ceramius hispanicus* standing on the wet ground at the stream during water uptake (note extended glossa). 4, Nest No. 4 of *Ceramius hispanicus* after excavation on 26 June, 1998 (turret removed, shaft filled with Maizena®; s = main shaft; c = constructed mud cell). 5, Constructed mud cells of nest No. 3 of *Ceramius hispanicus* on 29 June, 1998 (length of scale bar 5 mm).



Fig. 6-10. 6, *Ceramius hispanicus* female during nest excavation. The female had backed out of the entrance with the soil-pellet held in her mandibles and was about to turn round and start the pellet discard flight. The nest entrance is surmounted by three elongated, distally converging processes (= p; third process mainly hidden by the middle one) (see also Fig. 11). 7, Female of *Ceramius hispanicus* initiating the turret at the entrance of the main shaft (mud pellet supported by mid-legs on the outside). 8, Female of *Ceramius hispanicus* placing a mud pellet on the distal end of one of the processes of the turret. 9, Copulation of *Ceramius hispanicus*, male and female grappling on the ground. 10, Copulation of *Ceramius hispanicus*; male still connected to the female by its genitalia after it had lost its hold on the thorax of the female that had tried to escape. The situation lasted for about 180 s.

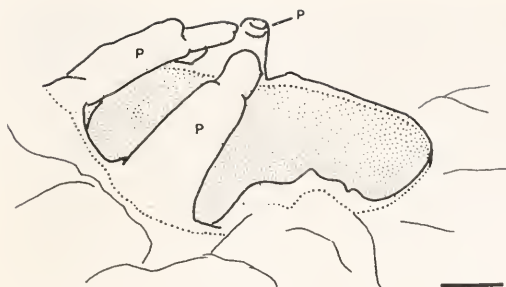


Fig. 11. Schematic representation of the nest entrance of *Ceramius hispanicus* (see also Fig. 6) (weakly dotted area = parts of the nest entrance which are made out of mud by the female; p = elongated, distally converging processes probably homologous with the turret; length of scale bar 1 mm).

northeast, gently sloping towards the latter. The nesting area measured about 2 m², its ground cover was 40–50%. The minimum distances between the nests varied from 0.4 to 1.2 m (median 0.7 m). Four nests were situated on the face exposed to the south-east and one was on top of the bank.

Nest architecture.—All nest entrances were to some extent hidden under leaves of plants. The entrance was surmounted by a low turret which was built of mud pellets cemented together. It consisted of a short basal ring which continued into the lining of the shaft towards the base. Distally, three elongated, converging, column-like processes arose obliquely from the basal ring (Figs 6, 11). The processes were about 3 mm long and were situated around that half of the entrance which was situated above the outside bend of the oblique outset of the shaft forming a three-pronged hood. Basally the processes were separated from each other by gaps of ca. 1 mm.

The shaft ran obliquely downwards at an angle of ca. 45° for the first 2–3 mm (Fig. 12). Below this it continued downwards more or less vertically for 40–60 mm, except in nest No. 2 in which the shaft descended obliquely to avoid stones (Fig. 12). This section of the shaft was 5–6 mm in diameter. The remaining part of

the shaft was obliquely or vertically orientated and was not terminated by a cell. It widened to 9–10 mm in diameter in the region of the brood cells which lay horizontally to sub-horizontally and radiated out from the main shaft. Secondary shafts were lacking so that the cell openings were directly integrated into the wall of the shaft. The constructed mud cells could be easily separated from the adhering soil (Fig. 4). The cells were elongate, more or less straight and noticeably wider at mid-length than before and after it; the inner end was markedly rounded (Fig. 5). Their outer surface was irregular but more or less homogenous (Fig. 5); the inner surface was smooth but dull. Measurements of each cell and details of its contents are listed in Table 1. The cell provision was a firm and relatively dry pollen and nectar loaf which did not adhere to the wall.

Nest-building behaviour.—Initiation of a nest by a female was observed three times. The females were flying slowly low over the ground. They interrupted their flight several times to alight on the ground which in some instances they scratched with their mandibles. At the future site of its nest, each female flew up from the ground and performed a circular orientation flight, the diameter of which was about 1m. Then the female alighted on the same spot again and directly started excavation.

Excavation was initiated by softening the soil with a liquid which was apparently regurgitated. A pellet of mud was formed by the mandibles; scratching movements of the fore- and mid-legs were performed in addition. When a pellet had attained about half the size of the head the female flew up with the pellet held between her mandibles. She flew very rapidly about 0.1 m above the ground towards an area situated between 0.3 to 0.7 m away from the nest in the immediate vicinity of a plant. At the end she hovered for a short moment, dipped down a few centimetres while dropping the pellet, re-

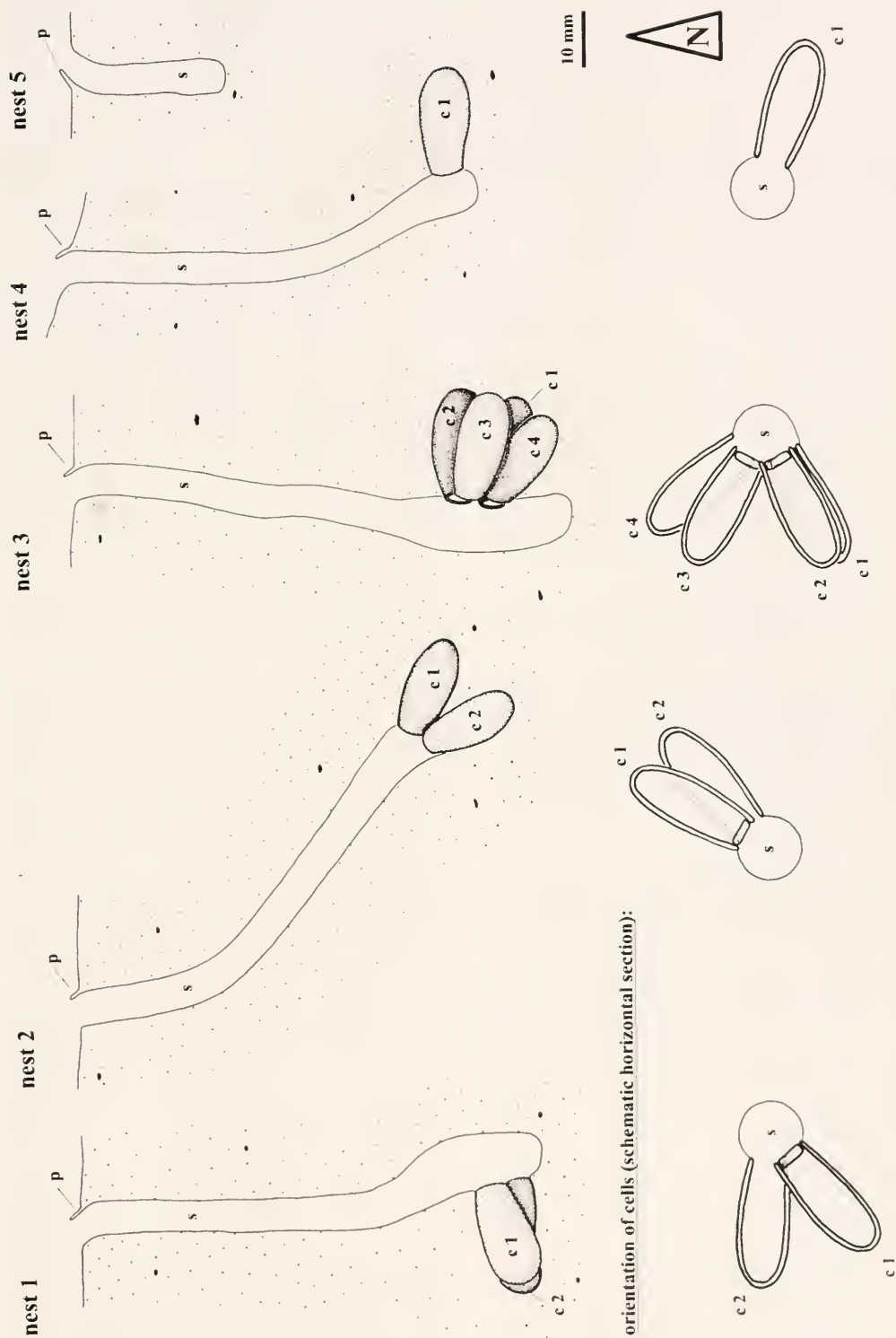


Fig. 12. Vertical plans of five nests of *Ceramius hispanicus* and plan views of the brood-cell arrangement (s = main shaft; c = constructed mud cell; p = distally converging median process of the turret; for further information see Table 1).

Table 1. Details pertaining to the five nests of *Ceramius hispanicus* excavated on 26 June, 1998 at Barranco de Zorita (measurements of cells and investigation of cell content were made on 29 June, 1998).

Nest data				Details of cells							
Nest no.	Date of founding	Σ females	Σ cells	Cell no.	Orien-tation	Depth below the sur-face of the ground (mm)	Exter-nal length (mm)	Exter-nal width (mm)	Inn-er diamet-er of cell open-ing (mm)	Condition	Content
1	22.06. 11h25	1	2	1	230°	73	?	?	?	sealed	small larva on pollen loaf
				2	275°	77	19.4	8.4	4.0	open	egg underneath pollen loaf
2	22.06. 12h47	1	2	1	30°	58	22.4	8.6	4.1	sealed	small larva laterally at the bottom of pollen loaf
				2	50°	64	21.0	8.2	4.3	open	egg underneath pollen loaf
3	22.06. 13h45	1	4	1	245°	69	17.3	8.4	4.1	sealed	larger larva below the pollen loaf
				2	245°	63	20.4	8.8	3.8	sealed	small larva laterally at the bottom of pollen loaf
				3	300°	66	17.5	8.8	3.8	sealed	small larva laterally at the bottom of pollen loaf
				4	320°	72	19.8	8.2	3.8	open	egg ± laterally from pollen loaf
4	23.06.	1	1	1	110°	63	20.4	8.8	4.2	open	small larva laterally at the bottom of pollen loaf
5	26.06.	1	0								

turned to the previous flying height again and flew rapidly back to the nest-initial. The female repeated the whole sequence of pellet formation and pellet dropping several times, in which always the same

Table 2. Flower-visiting records for males and females of *Ceramius hispanicus* during 11 hours of observation on three days at Barranco de Zorita (the number of flowers visited per plant is not taken into account).

Plant taxon	Number of plants visited by	
	Males	Females
Lamiaceae		
<i>Nepeta nepetella</i>	5	
<i>Marrubium supinum</i>	4	7
<i>Sideritis spinosa</i>		1
<i>Thymus zygis</i>		1
Fabaceae		
<i>Lotus corniculatus</i>		7
Cistaceae		
<i>Helianthemum apenninum</i>		2
<i>Helianthemum cinereum</i>	1	
Asteraceae		
yellow <i>Cichorioideae</i> sp.	1	

area was used for pellet dropping. All females continued to use their individual pellet-dropping areas over the whole observation period until 26 June. Once it was observed that a stone which was obviously too heavy to be removed by a pellet dropping flight was carried away from the nest-initial on foot. Formation of a pellet took about 30 seconds. After a female had discarded three to five pellets she flew away from the nesting site, probably to collect water. On average females returned after 205 seconds (n = 6) and continued to excavate the entrance of the nest.

After 25 to 60 minutes of excavation shafts were sufficiently deep that an excavating female was no longer visible when she had entered the nest. An excavating female now had to back up the shaft with a pellet held between her mandibles. As soon as such a female had left the nest entrance she turned about 90° on her vertical axis and performed a pellet dropping flight as described before.

About 60 minutes after initiation of the

Table 3. Pollen composition of provision from nine brood cells from four nests of *Ceramius hispanicus* collected on 26 June, 1998 at Barranco de Zorita (n = 1500 pollen grains/provision).

Cell	Nest 1		Nest 2		Nest 3				Nest 4
	1	2	1	2	1	2	3	4	1
Cistaceae									
<i>Helianthemum</i>	94.3%	97.5%	61.9%	75.9%	97.7%	83.8%	64.8%	61.0%	94.9%
Primulaceae									
<i>Coris</i>	1.2%	1.3%	12.1%	6.1%	1.6%	15.2%	33.8%	34.4%	1.0%
Lamiaceae									
four species	0.7%	0.9%	15.0%	11.8%	0.6%	1.0%	1.0%	2.4%	3.0%
Fabaceae									
<i>Lotus</i>	3.8%	0.3%	9.7%	6.0%				0.7%	0.4%
Convolvulaceae			0.2%	0.1%	0.1%		0.3%	0.5%	0.1%
Crassulaceae								0.8%	0.1%
unknown pollen			1.1%	0.1%			0.1%	0.2%	0.5%
Σ	100%	100%	100%	100%	100%	100%	100%	100%	100%

nest a female started to build a turret. At this stage when she backed up the shaft with a soil pellet held between her mandibles she held on to the ground around the rim of the entrance with her hind legs with her venter positioned outwards (Fig. 7). The wet soil pellet was placed on the rim of the entrance of the shaft and worked with the mouthparts from the inside while it was supported on the outer surface with the mid-legs (Fig. 8). Finally the female entered the shaft again and the whole sequence started anew. On a few

occasions the female curved the metasoma around while placing a pellet so that the pellet was obviously supported on its outer surface by the ventral surface of the tip of the metasoma and the mid-legs. After about 15 minutes (interrupted by water collecting flights) the turret was completed and the female resumed excavating the nest as before (Fig. 6). The turret of nest No. 1 was immediately rebuilt to similar design by the female after it had been experimentally destroyed on 23 June.

The females always entered the nest

Table 4. Pollen composition of gut content of five males and five females of *Ceramius hispanicus* collected at Barranco de Zorita (n = 100–250 pollen grains/individual; dbM No. = serial number in the database of V.Mauss, repeated on the determination labels).

dbM No.	Females					Males				
	1419	1421	1424	1430	1432	1418	1426	1435	1441	1442
Cistaceae										
<i>Helianthemum</i>	23%	97%	18%	65%	69%	74%	27%	40%	52%	56%
Primulaceae										
<i>Coris</i>	7%			5%	25%	1%	2%			
Lamiaceae										
<i>Sideritis</i>	28%	3%	15%	10%	3%	16%	38%	2%	15%	3%
<i>Marrubium</i>	1%						6%		1%	34%
other taxa	26%		56%	18%		2%		56%	29%	4%
Fabaceae										
<i>Lotus</i>	14%			1%						
Asteraceae										
<i>Anthemis</i> -type			5%				18%	1%		
Coniferopsida			4%	1%	2%	4%	7%	1%	2%	2%
unknown pollen	1%		2%		1%	3%	2%		1%	1%

head first. They were able to turn around inside the nest, but during excavation they left the entrance always backwards.

Water collection.—Females alighted frequently at the edge of the little stream or on the damp soil in its immediate vicinity to collect water. They were never observed to settle on the water surface. After landing the females often walked a few steps forward, stopped, extended the glossa and started to take up water, this being accompanied by vigorous pumping movements of the metasoma (Fig. 3). During water-collection females often chose spots on the damp soil or at the edge of the water, which were hidden by vegetation. Females were observed much less frequently at the two ponds and the trough than at the stream. Females visiting the ponds stood on the blades of the rushes during water uptake; at the trough they held on to the vertical walls a short distance above the surface of the water.

Forage plants.—Flower-visiting records for imagines are summarized in Table 2. Males visited the flowers of the Lamiaceae extensively while the observed single visits to *Helianthemum cinereum* and the yellow Asteraceae were very short. The females were observed to visit mainly white flowering Lamiaceae and *Lotus corniculatus*. Three times females were observed to change from one plant taxon to another during a single foraging trip, indicating low flower fidelity. The behavioural pattern exhibited on flowers differed remarkably with the plant taxon. While visiting flowers of Lamiaceae the imagines inserted the mouthparts and the distal parts of the head deeply into the corolla. On one occasion it was seen with certainty that the glossa was extended when the head was removed from the flower, indicating nectar uptake. When females alighted on flowers of *Lotus corniculatus* the alae of the flower were pressed ventro-laterally. Simultaneously, the females performed lateral movements with the gaster and moved the distal parts of the forelegs al-

ternately underneath their body. The foretarsi were brought to the mouthparts a few times during the process, indicating pollen uptake. When on flowers of this plant species, the females were never observed to insert their heads into the corolla base.

The brood cells were provisioned with a firm and relatively dry loaf composed of nectar and pollen. The pollen composition of all provision sampled was remarkably similar. All provision contained high percentages of pollen of *Helianthemum apenninum* and *H. cinereum* (Tab. 3); less important pollen sources though well represented in some brood cells were *Coris monspeliensis*, four different species of Lamiaceae, and *Lotus corniculatus*. Pollen of Convolvulaceae and Crassulaceae occurred in small amounts in some cells. Likewise, the alimentary tract of the imagines contained pollen grains of *Helianthemum*, *Coris*, several species of Lamiaceae, and *Lotus*; pollen of Asteraceae occurred in addition (Tab. 4).

Mating behaviour.—Males were most frequently observed at water. They flew in elliptic flight paths along the stream banks in a slow, constant flight about 0.1 m above the ground. The most striking feature of the flying males was the white coloration of the clypeus and the mandibles, which strongly contrasted with the dark coloration of the body. In addition, the antennae, raised at about 45° to the median axis of the body, showed their conspicuously orange-marked curved distal ends. The patrolling males sometimes interrupted their flight and alighted on sun-exposed stones which were situated 0.1 to 1 m (exceptionally 3 m) away from the stream. On the perch the males maintained a characteristic posture. Antennae and wings were raised at about 45° to the median axis of the body; the head was often slightly raised; and the mandibles were usually closed, although it was observed a few times that the glossa was stretched forward slightly (Fig. 2). Perch-

ing males occasionally rubbed the metasoma ventrally and laterally by alternate movements of the hind-legs, or they groomed the head, the thorax and the antennae by alternate movements of the fore-legs. The frequency of perching and the time spent on a perch decreased during the day. In the morning, males stayed for up to 60 s on a perch whereas males alighted only for a few seconds later in the day. Interactions between males were observed occasionally. Two incidents were observed of two patrolling males rapidly approaching each other, falling to the ground, grappling there for a short time and finally separating and flying away. Flying males were also observed to approach perching males resulting in the departure of the latter from the perch, followed by contact in the air, grappling on the ground, and finally separation.

Copulatory attempts were frequently observed at the edge of the stream. Patrolling males approached females which were on the ground collecting water. Males were often observed to turn away after they had nearly reached the females but before coming into contact with them. However, they also frequently pounced on sitting females, vigorous grappling on the ground following (Fig. 9). Insertion of the male genitalia was observed with certainty on three occasions although it probably occurred more often. On one occasion the male lost its hold on the thorax of the female during insertion and held on to a plant while the female tried to escape. The couple was still connected by the genitalia and remained in this position for a further 180 s (Fig. 10). Often the pairs separated after a short spell (1–5 s) of grappling on the ground but some copulations lasted a few minutes, at most six. Pairs never flew off together during copulation but always separated on the ground before they departed independently.

Males also patrolled along plants in a slow, constant flight. Patrolling males were mainly observed in the afternoon at

patches of *Marrubium supinum* about 50 m away from the nesting aggregation. Between 8h00 and 9h00 on 22 June two searching males were observed; between 14h00 and 16h00 eight records of at least six different patrolling males (marked or collected) were made and five females were observed visiting the flowers. No resightings occurred. Copulations were not observed but twice a male briefly approached and followed a honeybee worker (*Apis mellifera* L.). On 23 June one or several males were repeatedly observed patrolling over the nesting aggregation and the adjacent vegetation at 12h40.

Activity pattern of males and females at water.—The results of the activity measurements are summarized in Figure 13. On both days females collected water after 12h30 more frequently than expected (Chi-Square test; $p \leq 0.001$). In contrast the activity of males and the frequency of copulatory attempts was significantly higher before 12h30 (Chi-Square test; $p \leq 0.001$ and $p \leq 0.01$ respectively) and declined in the afternoon. Males were observed to perch more often in the morning than later in the day but this was only significant on 21 June (Chi square test; $p \leq 0.001$; $p = 0.06$ for 24 June). The first male appeared at the stream at 7h36, the first female at 7h43. Males were not observed after 17h20 whereas females collected water until 18h03.

Associated organisms.—A female of a bee (probably *Lasioglossum* sp., Halictidae) was hiding in cell No. 2 of nest No. 1 on June 26. It escaped during excavation.

DISCUSSION

Nest construction.—All species of *Ceramius* for which nesting is known construct a cylindrical turret surmounting the nest entrance (Gess and Gess 1988, 1992, Mauss 1996a). The presence of a turret-like structure in *C. hispanicus* is therefore considered to be a plesiomorphic trait, although the shape of the turret is strongly derived. The homology of the structures is

supported by their identical position at the nest entrance and the strong similarities in the behaviour of turret-construction (cf. Gess and Gess 1980). A possible function of the three converging processes of the turret of *C. hispanicus* may be to camouflage the nest by disguising the contour of the entrance hole. Thereby the nest is nearly invisible to potential vertebrate predators, made more so by hiding the entrance under leaves.

The burrow of *C. hispanicus* differs from that of *C. tuberculifer* (cf. Giraud 1871, cf. Mauss 1996a) and the majority of the Afrotropical *Ceramius* (Gess and Gess 1986, 1988, 1990, 1992) in that the main shaft is not terminated by a cell, a situation which is probably apomorphic. Within the ground-nesting Masarinae lack of a terminal cell at the end of the main shaft is only known for *Ceramius lichtensteinii* (Klug) (Gess and Gess 1980), *Paragia tricolor* Smith (Houston 1984) and *Jugurtia confusa* Richards (Gess and Gess 1980). A further derived character of the nest of *C. hispanicus* is the absence of secondary shafts which are reported to occur in all ground-nesting Masarinae for which nests with more than one cell have been found (cf. Gess 1996: 66 ff., 1999, Gess et al. 1995, Mauss 1996a). As in members of the Afrotropical species-groups 3 and 6 the main shaft of the nest of *C. hispanicus* is enlarged at or near its base. In the remaining taxa of *Ceramius* the main shaft shows a short bulbous enlargement at mid-length (Gess and Gess 1980, 1986, 1988, 1990, 1992) or is not enlarged (Gess 1999, Mauss 1996a). The "bulb" probably allows the imagines to turn around in the shaft (Gess and Gess 1988). Lack of a defined bulb in *C. hispanicus* and *C. tuberculifer* (Mauss 1996a) may be functionally correlated with the comparatively short length of the main shaft which causes the basal turning area to be situated in a tolerable distance to the entrance.

The dimensions of the burrow of *C. hispanicus* and *C. tuberculifer* (cf. Mauss

1996a) are quite similar, but they differ in that the main shaft normally descends more or less vertically in *C. hispanicus* whereas it descends vertically (Giraud 1871) or obliquely to sub-horizontally (Mauss 1996a) in *C. tuberculifer*. The differences may only be modifications related to the nature of the substrate at the nest site. In contrast to *C. tuberculifer* (Mauss 1996a), the main shaft of the nest of *C. hispanicus* is not terminated by a cell. Within *Ceramius* this condition is merely known from *C. lichtensteinii* (Gess and Gess 1988, Gess 1996, Gess 1999) the only member of species-group 5. The existence of constructed mud-cells (sensu Gess and Gess 1986) which are presumably built within an excavated cell and the sub-horizontal orientation of these cells can be assumed to be plesiomorphic traits of *C. hispanicus* which are adopted from the ground-pattern (sensu Ax 1984: 156) of *Ceramius*. They exist in the majority of species of *Ceramius* and are also present in some *Paragia* (cf. Houston 1984, 1986) and *Jugurtia* (Gess and Gess 1980, Gess 1996: 95).

Digging females of *C. hispanicus* use a clearly defined pellet-dropping area over successive days. A set pellet-dropping area is also used by *C. tuberculifer* (Mauss 1996a), *C. rex* Saussure, *C. metanotalis* Richards, *C. bicolor* (Thunberg), *C. capicola* Brauns and *C. socius* Turner (Gess 1996, Gess and Gess 1980, 1988), whilst females of other *Ceramius*-species spread out the pellets over a larger area (Gess and Gess 1980, 1988). All species of *Ceramius* discard pellets in flight, with the exception of *C. tuberculifer*, the females of which move to the pellet-dropping area on foot (Mauss 1996a). The pellet-dropping area of *C. hispanicus* is situated farther away from the nest entrance than in the remaining five species using a defined pellet-dropping area (cf. Mauss 1996a, cf. Gess and Gess 1980, 1988). *C. hispanicus* utilizes a liquid to soften the soil in nest construction. This liquid is probably water since water is frequently collected by the females. Usage of

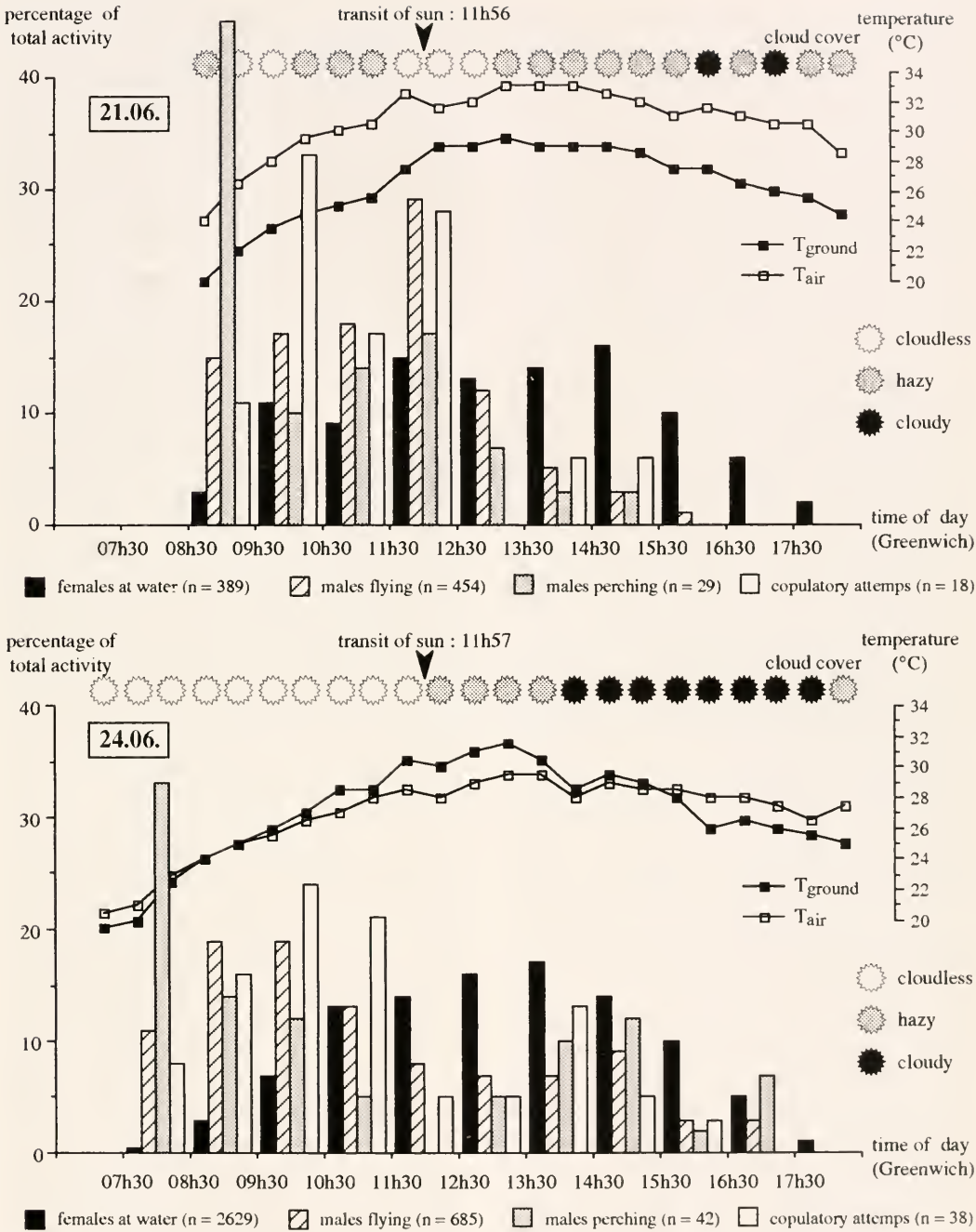


Fig. 13. Activity pattern of males and females of *Ceramius hispanicus* on 21 June and 24 June, 1998 at a little stream in the Barranco de Zorita (prov. Teruel, Spain). The proportion of the summed activity of each hour to the amount of activity of the whole day (= n) is plotted against the time of the day for each category. The line chart shows the temperature changes over the day; covering of clouds is expressed by symbols (for further details see text).

water in nest building has been reported for all Afrotropical *Ceramius* and *C. tuberculifer* (Gess and Gess 1980, 1986, 1988, 1990, Gess 1996, Ferton 1901), although the latter species may use nectar instead (Mauss 1996a). During water collection the females of *C. hispanicus* land on very wet ground or at the edge of a water source. Standing on the ground during water uptake occurs in species-group 2 as well, while members of species-groups 3, 4, 5, and 6 stand on the surface of the water (Brauns 1910, Gess and Gess 1988, 1990, Gess 1996: 76, 1999). Group 8 is exceptional in showing inter- and intraspecific variation in water-collecting behaviour (Gess 1996: 76). Nothing is known about the functional significance of the different water-collecting strategies. The observed vigorous pumping movements of the metasoma of the females during water uptake may serve to eliminate air from the anterior air-sacs to make some space for the dilatation of the crop. However, they may also turn out to be normal respiratory movements after a flight.

Perennial re-use of nests has been recorded for most Afrotropical species which construct mud-cells and *C. tuberculifer* (Gess and Gess 1988, Gess 1996, Mauss 1996a). Reuse of nests by *C. hispanicus* can not be excluded, but it is remarkable that all the nests examined were newly founded. The cell-construction rate of *C. hispanicus* can be roughly estimated from the field data. Based on the present sample, a female starting a new nest can be expected to construct, provision and seal 0.5 (range 0.3 to 0.9) cells per day (open cells were calculated as 0.8 cells). Comparable data are not available for other ground-nesting masarines. The aerial nesting *Celonites abbreviatus* (Villers) was observed also to finish about 0.5 cells per day (calculated from Bellmann 1984).

Forage plants.—*Ceramius hispanicus* is broadly polylectic and capable of dealing with flowers of very different architecture. In the study area the main pollen sources

are *Helianthemum* (Cistaceae) and *Coris* (Primulaceae), to a lesser extent also *Lotus* (Fabaceae) and four species of Lamiaceae. Furthermore, pollen of Crassulaceae and Convolvulaceae is used in small amounts and the occurrence of pollen of Asteraceae in the alimentary tract of males and females indicates that pollen of this family might be used for larval nourishment as well. Flowers of *Helianthemum* exclusively provide pollen (Kugler 1970: 206), so that the females have to take nectar from other plants. Nectar seems to be mainly collected from flowers of various Lamiaceae which is indicated by a high proportion of flower-visiting records being for Lamiaceae despite the comparatively low quantity of pollen of Lamiaceae present in the provisions of the brood cells or in the alimentary tract. Males also consume large amounts of *Helianthemum* pollen indicating that they do not incidentally ingest pollen during nectar uptake but actively feed on it. As already established by Gess & Gess (1988) pollen analysis is the only reliable method to elucidate pollen-plant preferences of masarine wasps.

Some of the remaining members of *Ceramius* species-group 7 are also polylectic. *Ceramius tuberculifer* consumes pollen of Lamiaceae, Cistaceae and Fabaceae (Mauss 1996a) and other members of the *C. lusitanicus*-complex have been recorded visiting flowers of Lamiaceae, Fabaceae and Apiaceae (Richards 1963). The main pollen source of *C. tuberculifer* is *Teucrium montanum* L. (Lamiaceae) and the imagines exhibit behavioural adaptations to the nototribic pollen presentation of Lamiaceae (Mauss 1996a). Such behavioural adaptations seem to be lacking in *C. hispanicus* which uses flowers of Lamiaceae mainly as a nectar source. Afrotropical species of *Ceramius* have not been recorded even as casual visitors of this family (Gess 1989, 1996) with the exception of *Ceramius damarinus* Turner the imagines of which use flowers of Lamiaceae as a nectar source (Gess 1999). It still remains un-

certain whether polylecty is a character of the ground pattern of species-group 7 or if it evolved within the group, as *Ceramius auctus* (F.) which diverged comparatively early may be restricted to Asteraceae (Mauss 1998). In contrast, the Afrotropical species of *Ceramius*, like the majority of the Masarinae (Gess 1996: 46–47), are markedly oligolectic (Gess 1989, 1996: 41) using only pollen of Asteraceae, Aizoaceae or Fabaceae. Furthermore, preferences for single plant families are characteristic at the species-group level in Afrotropical *Ceramius*.

Mating system.—Mate location behaviour of males of *C. hispanicus* includes perching and patrolling at water-collecting sites and also patrolling along flowers of Lamiaceae at times when these are visited by the females. This is confirmed by observations made at Valdelobus (Teruel) where males also patrolled along the edge of a stream and along *Marrubium supinum* (Mauss unpubl.). Multiple encounter sites are common for various aculeate Hymenoptera (Alcock et al. 1978, Eickwort and Ginsberg 1980), however, most cases involve only nesting areas and flowers. *Ceramius* like *Paragia* utilizes three potential encounter sites: nesting areas, flowers and water collecting sites (cf. Gess and Gess 1990, cf. Gess 1996: 59 ff., cf. Houston 1984, cf. Naumann and Cardale 1987). Mate-seeking both at flowers and at water has only been recorded for five Afrotropical species of *Ceramius* (Gess and Gess 1990, Gess 1996: 61, Gess 1999). In *C. hispanicus*, preference for one of the encounter sites seems to be correlated with time of the day. Males are most active at water in the morning, where their activity declines during the day, but they patrol more frequently at flowers in the afternoon. However, total activity of males is much lower at flowers than at water and copulatory attempts were only observed at the latter. Interestingly enough, the males of *C. hispanicus* encountered females at their main nectar sources and not at the

pollen plants. Possibly the probability of a male encountering a female was higher at the nectar-plants, species of Lamiaceae, since these were more aggregated in the study area then were the major pollen-plants which were scattered. Within the patches of Lamiaceae the density of flowers was comparatively high, so that a male could patrol along higher numbers of flowers per unit time than in the more evenly distributed pollen plants, like e.g. *Helianthemum*.

At water, mating occurs more frequently in the morning than in the afternoon which corresponds well with the observation that males appear earlier than females. The decline of male activity in the afternoon is probably not the result of changes of the abiotic conditions, since female activity increases during the day and the fewer males observed still behaved as before. Two reasons should be considered. First, the males may require nectar since they have depleted their energy reserves and secondly, the number of virgin females may decline during the day due to the mating effort of the males. A comparable activity pattern is exhibited by males of the Australian masarine *Paragia tricolor*, which Houston (1984) observed flying around shrubs between 8h30 and 14h00 diminishing in numbers after midday. Males of *C. tuberculifer* were observed to patrol along flowers between 10h30 and 14h00 (Mauss 1996a). At water, the males of *C. hispanicus* alternate between perching and patrolling. The proportion of perching to patrolling is highest at the onset of the daily flight period and declines rapidly thereafter. This may be correlated with rising temperature (cf. Alcock et al. 1978), but as the males are active ahead of the females it could be the arrival of the females which prompts this behavioural change as well. The few incidents of grappling between males indicate that some kind of territoriality is involved in the mating system (cf. Eickwort and Ginsberg 1980). It is important to emphasize that the

males probably did not mistake each other for a female, since all combats started in the air. In contrast, patrolling males were never observed to approach flying females, but frequently pounced on females sitting on the ground. Important visual signals which enable the males to recognize each other possibly come from their distinct coloration of head and antennae. During mating, the males grappled vigorously with the females giving the impression of a forced copulation. This could indicate that the majority of the females had been inseminated already. On the other hand it may be possible that the females test the potential fitness of a male by offering resistance.

Knowledge about the daily period of flight activity of *Ceramius* is very fragmentary. *C. hispanicus* seems to be unusual in that its activity lasts for about 10 hours being from 8h00 to 18h00 and imagines are not much affected by some cloud cover. Females even collected water in the evening after the stream was completely shaded by the ridge of the mountains. In contrast the active period of the Afrotropical species and of *C. tuberculifer* seems to be shorter (Gess and Gess 1980, 1990, Mauss 1996a) and their imagines are very sensitive to less favourable weather conditions in general and disappear quickly when the sun is obscured by cloud or a breeze gets up (Gess and Gess 1980, Mauss 1996a).

Associated organisms.—Presence of female halictine bees in nests of *Ceramius* has also been recorded for *C. lusitanicus* (Klug) (Mauss, unpubl.), the nests of which they were observed to appropriate.

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Revision of the Australian Tiphid Genus *Leiothynnus* (Hymenoptera: Tiphidae: Thynninae)

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Abstract.—The Australian thynnine genus *Leiothynnus* Turner is revised, describing five new species from Queensland, including *cardalae*, *ferricolus*, *linnis*, *multimaculatus* and *ochrotarsus*, and two previously described species, *mackayensis* (Turner) and *spinigerus* Turner, also from Queensland. Distribution maps of species and a key to males are given.

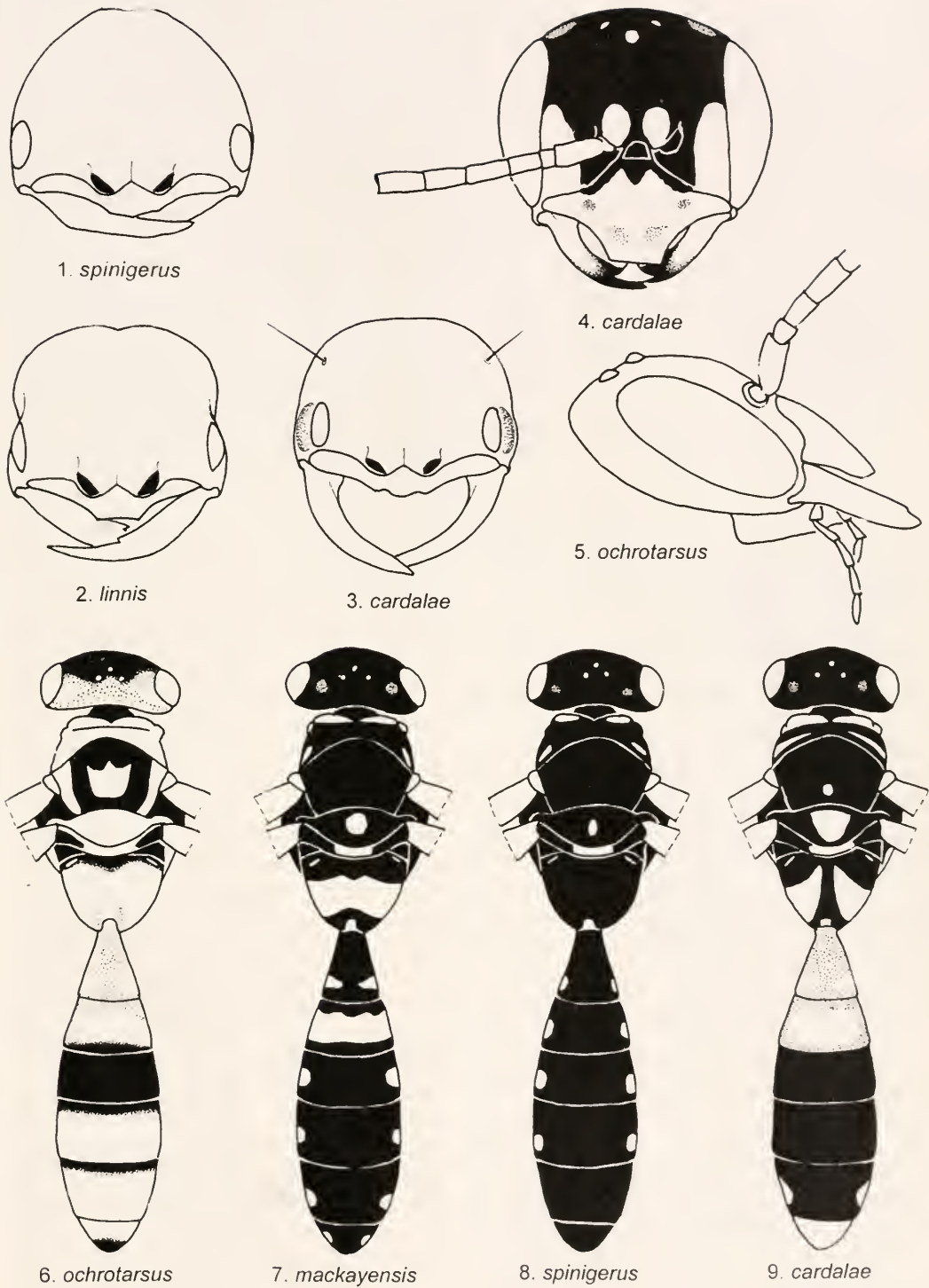
Most Australian genera of Thynninae are widespread, occurring in many Australian states, with some even extending up into New Guinea, New Caledonia and adjacent islands. However, there are some small genera with relatively restricted distributions, such as *Oncorhinothynnus*, which is only found in west central Western Australia, or *Gymnothynnus* Turner, from Northern Territory and western Queensland. The genus *Leiothynnus* Turner is one of these relatively localized groups. All *Leiothynnus* species have been collected from eastern Queensland. In addition to the two described species, *mackayensis* (Turner) and *spinigerus* Turner, there are five new ones, which are described below.

The specific relationships between *Leiothynnus* and other thynnine genera are not fully resolved. *Leiothynnus* shares a number of features with *Isvaroides* Ashmead and *Epactiothynnus* Turner, including in the male the well-developed and somewhat arcuate penis valves, volsella U-shaped in cross-section, stipes arcuate with long marginal fringe of setae, vertex with small reddish spot behind the dorsal eye margin, and a large oral plate. In the female, the pygidium has two submedial longitudinal carinae, subtended by a long tuft of setae. A few characters are shared

with *Agriomyia* Guérin de Meneville, including the flat male face (Fig. 5), with extreme reduction of the antennal lobes, and simple male epipygium, lacking the well-developed transverse carina or ridge typical of *Epactiothynnus* and related genera. However, remnants of this ridge can be seen, particularly in *cardalae* and *ochrotarsus*. *Leiothynnus* can be distinguished from these and other genera by the long brush of setae on the base of the male prementum, the darkly stained marginal cell in the forewing, and slender, petiolate male abdomen.

Leiothynnus species differ from one another in modifications of the male legs, abdominal apex and to some extent color. All of the species treated below have the male thorax with dense, nearly contiguous punctation, and the propodeal punctation obscured by fine shagreening. These features may or may not be significant at the species level. Collecting seems to be too patchy to say whether or not there are additional undescribed species. Too few females have been collected to generalize about diagnostic features among the species in females, although there appear to be differences in the overall shape of the head and development of carinae or lobes on abdominal segment V.

Specimens were obtained from the fol-



Figs. 1-9. *Leiothymus* species. 1-3, Front view of female face, antennae removed. 4, Front view of male face, right antenna removed. 5, lateral view of male face. 6-9, Dorsal view of male body showing color pattern, white = yellow, black = black, stippled = orange to red; wings removed.

lowing institutions and individuals: The Australian National Insect Collection, CSIRO, Canberra, ACT, J. Cardale (CANBERRA); the Natural History Museum, London, England, S. Lewis; Queensland Museum, Brisbane, Australia, C. Burwell (BRISBANE-QM), and University of Queensland, Insect Collection, Brisbane, Australia, G. Daniels (BRISBANE-UQIC). Some paratypes will be deposited in the Bohart Museum of Entomology, University of California, Davis (DAVIS). The types of both previously described species were studied.

Leiothynnus cardalae Kimsey, new species

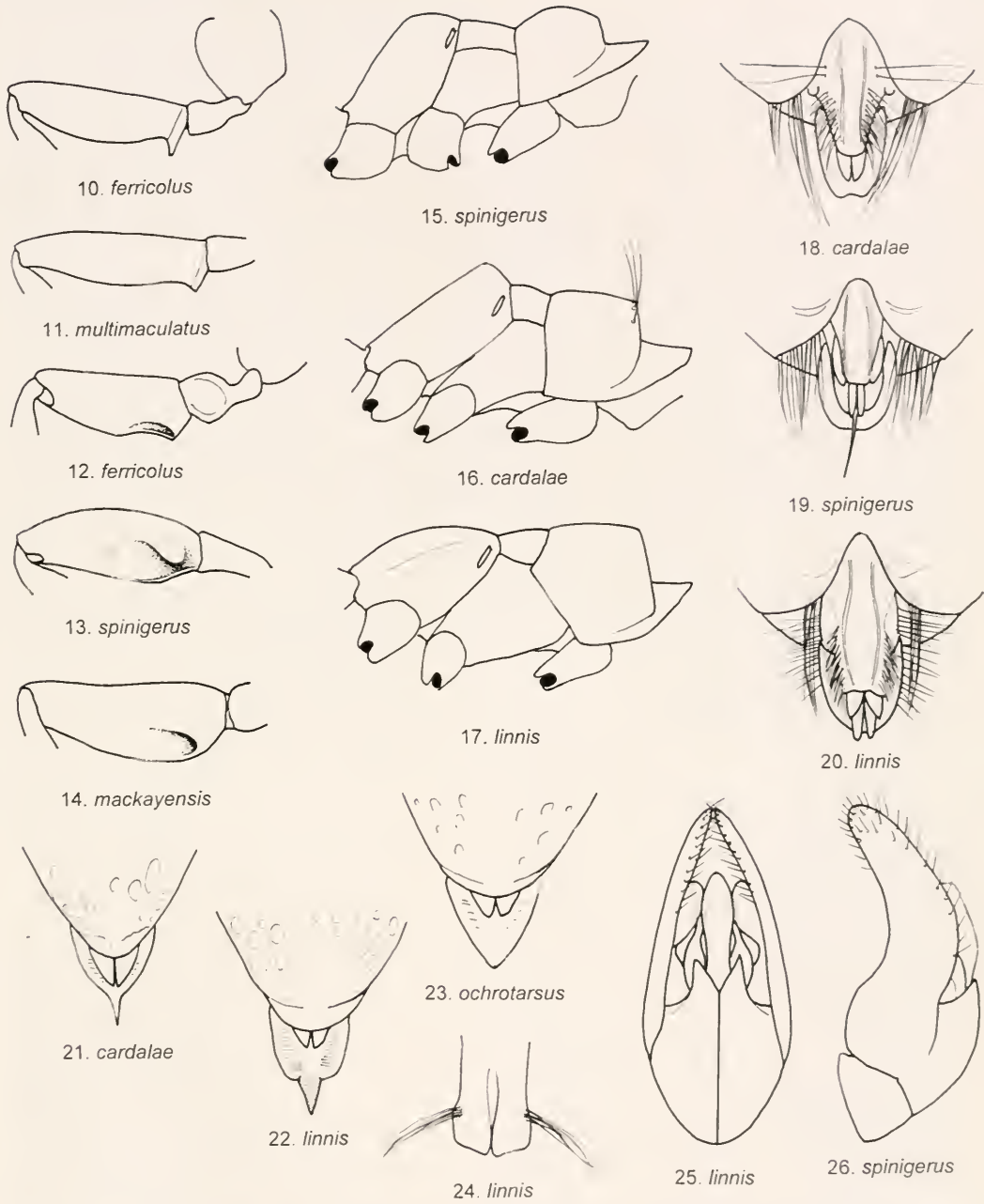
(Figs. 3, 4, 9, 16, 18, 21, 27)

Male.—Body length 7.5 mm. *Head*: face (Fig. 4) with dense small, nearly contiguous punctures; flagellomere I length $1.5\times$ breadth; flagellomeres II-III $2.5\times$ as long as broad. *Thorax*: punctures dense and nearly contiguous; propodeal punctures obscured by fine dense shagreening; scrobal sulcus strongly U-shaped, ventral loop sharply defined; foretrochanter convex in cross section; forefemur evenly convex basally, without carina, knob or other modification; midtrochanter and femur unmodified; midcoxal inner margin narrowly rounded, not angulate. *Abdomen*: hypopygial apex broadly rounded with short medial projection (projection often weakly sclerotized or translucent in some individuals) (Fig. 21). *Genitalia*: paramere arcuate, broadly rounded apically, broadest subapically (as in Figs. 25, 26). *Color* (Fig. 9): body black, with yellow and orange markings: head black with yellow clypeus, yellow along inner eye margin, between and across antennal lobes; scape pedicel and flagellomeres I-V red; rest of flagellum dark brown; pronotum black with yellow transverse anterior and marginal posterior bands; mesopleuron with subalar yellow spot and large yellow spot above midcoxa; one specimen with small yellow scutal spot; scutellum and metanotum with large

medial yellow spot; propodeum with large lateral yellow marks, narrowly separated medially; trochanter and femora reddish brown, femoral apices sometimes paler, tibiae red, tarsi yellow to cream-colored; tergum I orange with transverse subapical yellow band, narrowed medially; tergum II yellow with narrow dark brown bands along anterior and posterior margins; tergum III-IV entirely black; tergum V-VI yellow anteriorly with narrow blackish posterior band, or black with yellow lateral spot; tergum VII dark brown to black; sternum I blackish basally, orange apically with yellowish middle; sternum II orange; sterna III-VI black.

Female.—Body length 4 mm. *Head* (Fig. 3): broader than long, vertex somewhat concave, with long seta above each eye; genal area above mandible with carina extending the length of eye. *Thorax* (Fig. 16): pronotal disk abruptly elevated above collar, disk with longitudinal medial sulcus, anterior margin with six long hairs; scutellum about twice as broad as long, propodeum strongly convex dorsally and elevated above scutellum, bulging medially and flattened sublaterally, medial bulge with long erect hairs. *Abdomen*: tergum I with broadly W-shaped transverse sulcus; tergum II with four large transverse ridges; tergum V apicomediaally emarginate; tergum VI with narrow parallel-sided carina-edged medial plate, apically subtended by short dense tuft of setae (Fig. 18); sternum VI apicomediaally emarginate and thin-edged, with long brush of setae laterally and shorter brush apicomediaally. *Color*: dark reddish brown.

Type material.—Holotype δ : Queensland, Luster Creek, 8 km nw Mt. Molloy, 21–22 May 1980, I. Naumann and J. Cardale (CANBERRA). Seven paratypes—3 $\delta\delta$: Mt. Webb National Park, 15.04°S 145.07°E , 20–27 April 1981, I. Naumann; 1 δ , one η : Shipton's Flat, 15.47°S 145.07°E , 16–18 May 1981, I. Naumann; 1 δ : Coen, 13.57°S 143.12°E , 13 Jan.–25 Feb. 1994, malaise trap, Zborowski and McKay; 1 δ : Tol-



Figs. 10–26. *Leiothynnus* Figs. 10, 11, Lateral view of male forefemur and trochanter. 12–14, Lateral view of inner surface of male forefemur and trochanter. 15–17, Lateral view of female thorax, legs removed. 18–20, Posterior view of female pygidium. 21–23, Dorsal view of male epipygium and hypopygium. 24, Ventral view of female apical abdominal sternum. 25, Dorsal view of male genital capsule. 26, Lateral view of male genital capsule.

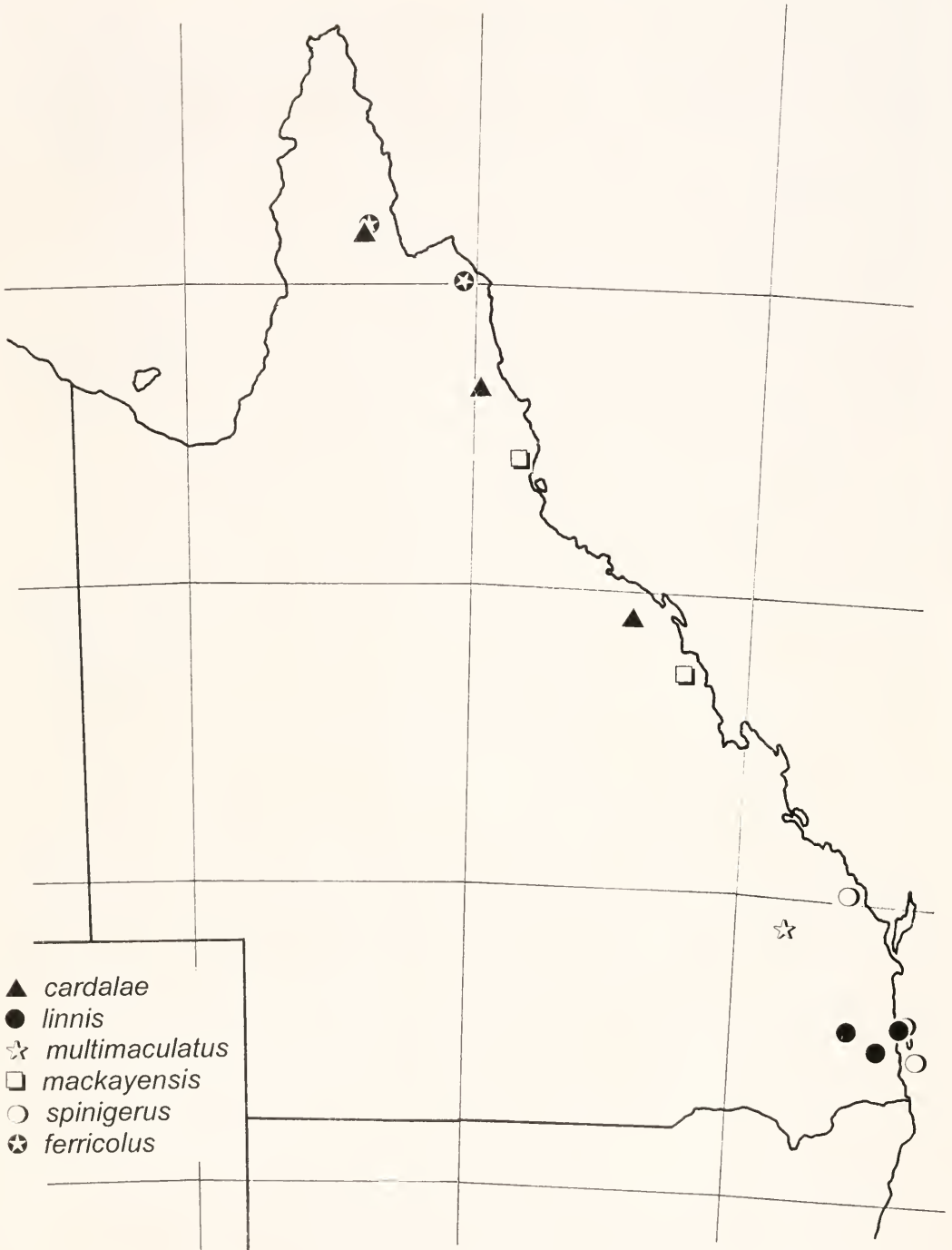


Fig. 27. Distribution map of six species of *Leiothynnus* in Australia.

ga, 3 Mar. 1964, R. Elder (BRISBANE-UQIC, CANBERRA, DAVIS).

Distribution.—Fig. 27.

Etymology.—This species is named in honor of Jo Cardale, who was one of the collectors of the holotype specimen. She also made much of this study possible, with collections support and encouragement overall.

Discussion.—*Leiothynnus cardalae* is a brightly colored species in the male, characterized by having a reddish brown to orange petiole. This coloration is shared with *ferricolus* and *multimaculatus*. Male *cardalae* can be distinguished by the unmodified fore- and midfemur (a characteristic shared with *ochrotarsus*), red legs and bicolored antenna. The female of *cardalae* has the least modified head of species where females are known. The female thorax is distinctive with a sparse row of long hairs along the anterior margin of the pronotum, strongly dorsally arched propodeum, and pygidium with lateral carinae parallel or converging slightly submedially, with a small lateral lobe on tergum VI.

***Leiothynnus ferricolus* Kimsey, new species**

(Figs. 10, 12, 27)

Male.—Body length 7.5–8.0 mm; punctuation as in *cardalae*. *Head*: flagellomere II 2.5× as long as broad; flagellomere III length 3× breadth. *Thorax*: scrobal sulcus with ventral loop poorly defined; foretrochanter strongly flattened and concave (Fig. 12); forefemur with short basoventral longitudinal carina, basolateral angle expanded and flattened ventrally (Fig. 12); midfemur with long basoventral tooth, tooth nearly as long as tarsal claw (Fig. 10), adjacent surface of trochanter flattened; midcoxa inner margin sharp-edged and angulate. *Abdomen*: hypopygial apex angulate laterally with long medial projection. *Genitalia*: as in Figs. 25, 26. *Color*: black with yellow and orange markings; clypeus yellow, interantennal area

yellow; inner eye margin with broad yellow stripe; mandible red with basal yellow spot; pronotum with broad transverse yellow anterior and posterior stripes; mesopleuron with large yellow subalar and supracoxal spots; scutellum and metanotum with large yellow medial spot; propodeum with large lateral yellow spots, narrowly separated medially; hindcoxa with yellow dorsal spot; trochanter and femora dark brown, femoral apices sometimes paler, orange; fore and midtibiae orange; hindtibia dark brown or orange; tarsi yellowish brown; wing membrane yellow stained; abdominal segment I black basally, becoming orange for most of length, with transverse yellow band or yellow spots; tergum II brown basally and apically with broad medially yellow band; sternum II brown with small lateral yellow spot; terga III, and in most specimens IV, black with small lateral yellow spot; terga V–VI black with large lateral yellow spot, spots sometimes convergent medially; tergum VII black to dark brown; sternum III–VII black.

Female.—Unknown.

Type material.—Holotype ♂: Queensland, Cape York Peninsula, Iron Range, Apr. 7–May 4, 1973, S. R. Monteith (CANBERRA). Nine paratype ♂♂: same data as holotype; 1 ♂: McIlwraith Range, 8 km ne Coen, 13°53.30S 143°15.21E, 13 Jan. 1994, G. & A. Daniels and R. Eastwood (BRISBANE-UQIC, CANBERRA, DAVIS).

Distribution.—Fig. 28.

Etymology.—This species is named after its collection locality the Iron Range; *ferrus* = iron, *icolus* = loving, Latin, masculine.

Discussion.—The most distinctive features of this species in the male are the cupped foretrochanter, basally carinate forefemur and long midfemoral tooth. Male coloration is very similar to that of *cardalae*, as discussed under that species.

***Leiothynnus linnis* Kimsey, new species**
(Figs. 2, 17, 20, 22, 24, 25, 27)

Male.—Body length 8–10 mm; punctuation as in *cardalae*. *Head*: flagellomere I

length $1.5\times$ as long as broad; flagellomeres II-III $2.2-2.4\times$ as long as broad. *Thorax*: scrobal sulcus U-shaped, ventral part weakly defined; foretrochanter convex in cross section; forefemur evenly convex basally, without carina, knob or other modification; midtrochanter unmodified, midfemur projecting basoventrally in right angle; mid- and hindcoxa inner margins broadly rounded, not angulate. *Abdomen*: hypopygial apex subtruncate, with strong medial projection (Fig. 22). *Genitalia* (Fig. 25): paramere arcuate, broadly rounded apically, broadest subapically. *Color*: body black with yellow markings: head black with yellow clypeus, yellow along inner eye margin and between and across antennal lobes; scape, pedicel and basal flagellomeres red; rest of flagellum dark brown; pronotum black, with yellow transverse anterior band and band along posterior margin; scutum with short yellow band adjacent to tegula; mesopleuron with subalar yellow spot and small yellow spot above midcoxa; mesopleural lamellae translucent with yellow margins; scutellum and metanotum with large medial yellow spot; propodeum with large lateral yellow marks, narrowly separated medially; trochanter and femoral base dark brown, femoral apices and rest of legs reddish orange; tergum I orange with transverse subapical yellow marks becoming darker basomedially, tergum II brown with broad transverse medial yellow band; tergum III-IV black without small yellow spot laterally; tergum V-VI yellow anteriorly, with narrow blackish posterior band, or black with yellow lateral spot (tergum V may also be entirely black); tergum VII brown becoming paler apically.

Female.—Body length 5–7 mm. *Head* (Fig. 2): slightly broader than long, strongly indented laterally above eye; vertex somewhat concave medially; genal area between mandible and oral fossa deeply longitudinally sulcate. *Thorax* (Fig. 17): pronotal disk abruptly elevated above collar, concave anteriorly; scutellum about

twice as broad as long, propodeum broad, slightly convex dorsally, nearly planar between petiolar socket and scutellum, strongly rounded laterally in dorsal view. *Abdomen*: tergum I with broadly W-shaped transverse sulcus; tergum II with four large transverse ridges; tergum V apicomediaally emarginate; tergum VI with narrow parallel-sided carina-edged medial plate with lateral upturned flanges, apical part subtended by long dense tuft of setae (Fig. 20); sternum VI apicomediaally notched, separated into two halves, by long ventral groove, with long brush of setae laterally, and shorter brush apicomediaally (Fig. 24). *Color*: dark reddish brown.

Type material.—Holotype ♂: Queensland, Brisbane, March (BRISBANE). Paratypes: 29 ♂♂, 8 ♀♀, same data as holotype; 1 ♂, 8.5 km sse Dayboro, $27^{\circ}16'S$ $152^{\circ}52'E$ (BRISBANE, DAVIS).

Distribution.—Fig. 27.

Etymology.—The species name, *linnis*, is a nonsense combination of letters and is assumed to be masculine.

Discussion.—The color and general appearance of this species are similar to *cardalae*. However, *linnis* can be immediately distinguished in the male by the unmodified forefemur and small basoventral angle on the midtibia, and in the female by the peculiarly modified head and ventrally divided apical abdominal sternum.

***Leiothynnus mackayensis* (Turner)**
(Figs. 7, 14, 27)

Thynnus mackayensis Turner 1908:123. Lectotype male (designated by Kimsey & Brown 1993); Australia: Qld., MacKay (LONDON).

Male.—Body length 9–10 mm; punctuation as in *cardalae*. *Head*: flagellomere I $1.5\times$ as long as broad; flagellomere II $2.5\times$ as long as broad; flagellomere III $3\times$ as long as broad. *Thorax*: scrobal sulcus U-shaped, ventral segment well-defined; foretrochanter convex in cross section; forefemur deeply cupped ventrobasally (Fig. 14); midtrochanter unmodified, mid-

femur with basoventral tooth, nearly as long as tarsal claw; midtrochanter unmodified; mid- and hindcoxaal inner margins broadly rounded, not angulate. *Abdomen*: hypopygium strongly exerted, apex apically rounded, with strongly sclerotized medial tooth. *Genitalia*: paramere arcuate, rounded apically (as in Figs. 25, 26). *Color* (Fig. 7): body black with yellow markings: head black with yellow clypeus, yellow along inner eye margin and between and across antennal lobes; mandible yellow, becoming reddish brown apically; scape, pedicel and flagellomere I red; rest of flagellum dark brown; pronotum with yellow transverse anterior band and posterior lobe adjacent to tegula yellow; mesopleuron with subalar yellow spot and large yellow spot above midcoxa; scutellum and metanotum with large medial and smaller lateral yellow marks; propodeum with large lateral yellow marks, narrowly separated medially; trochanters and most of femora dark brown, femoral apices and rest of legs reddish brown; terga I and III-IV black with small apicolateral yellow spot; tergum II with large lateral yellow spots nearly meeting medially; terga V-VII black; sterna black, although sternum II often with small yellow apicolateral spot; wing membrane yellow-tinted.

Female.—Unknown.

Material examined.—Australia: Qld, Dunk Is. and Mackay; 5 ♂♂ were seen including the lectotype.

Distribution.—Fig. 27.

Discussion.—Male *mackayensis* share their dark coloration with *spinigerus*, although unlike *spinigerus* this species has a yellow band across the propodeum and tergum II. *L. mackayensis* males can be readily distinguished from *spinigerus* and other species by the combination of the basally cupped forefemur (shared with *multimaculatus*), and strongly dentate midfemur (shared with *ferricolus* and *spinigerus*).

Leiothynnus multimaculatus Kimsey,
new species
(Figs. 11, 27)

Male.—Body length 11 mm; punctuation as in *cardalae*. *Head*: flagellomere I 1.5× as long as broad; flagellomere II 2.2× as long as broad; flagellomere III 2.5× as long as broad. *Thorax*: scrobal sulcus U-shaped with ventral part weakly defined; forefemur with deep U-shaped basoventral impression, with associated longitudinal carina (similar to Fig. 12); foretrochanter unmodified; midfemur with short basoventral tooth, one half or less as long as tarsal claw (Fig. 11), adjacent area on trochanter flattened; mid and hindcoxae without sharp inner margin, evenly rounded not angulate. *Abdomen*: hypopygium slightly flattened apically on either side of medial spine. *Genitalia*: as in Figs. 25, 26. *Color*: black with yellow and orange markings; clypeus mostly yellow; antennal lobes and subantennal sclerite yellow; inner eye margin with broad yellow band; mandible red with yellow basomedially; postocular margin with short yellow band; scape, pedicel and ventral surface of flagellomeres I-IV paler red; rest of flagellum black; pronotum with yellow band along posterior margin; mesopleuron with large yellow subalar spot; mesopleural lamella with whitish stripe along inner margin; scutellum and metanotum with large medial yellow spot; propodeum with large lateral spots, broadly separated medially; coxae black becoming reddish dorsally on mid and hindlegs; femora dark brown to black, becoming red apically; tibiae and tarsi red (except hindtibia darkened subapically in holotype); terga III-IV black without lateral yellow spots; tergum VI black with small irregular medial yellow spot; tergum VII black; sternum I orange; sternum II orange becoming darker apically with yellowish lateral spot; sterna III-VI black.

Female.—Unknown.

Type material.—Holotype ♂: Queens-

land, Rockpool Gorge, Bluff Range, near Biggenden, 4 Oct. 1976, H. Frauca (CANBERRA). Paratype ♂, Bluff Range, Biggenden, 9–20 Dec. 1972, H. Frauca (CANBERRA).

Distribution.—Fig. 27.

Etymology.—The species name is derived from the multicolored male; *multus* = many, *maculatus* = marks, Latin, masculine.

Discussion.—The most distinctive features of this species in the male are the ventrally cupped forefemur, small basal midfemoral tooth and associated indentation on the midcoxa, red legs and red basal abdominal segments. *L. multimaculatus* most closely resembles *mackayensis* but can be distinguished by the more extensive yellow and orange coloration and smaller midfemoral angle (as in Fig. 11).

***Leiothynnus ochrotarsus* Kimsey, new species**
(Figs. 5, 6, 23)

Male.—Body length 11 mm; punctuation as in *cardalae*. *Head* (Fig. 5): flagellomere I 1.5× as long as broad; flagellomere II length twice breadth; flagellomere III 2.3× as long as broad. *Thorax*: foretrochanter convex in cross-section; forefemur basally indented with short longitudinal carina; mesopleuron with ventral part of scrobal sulcus obsolescent; midfemur basoventrally with slight angle or unmodified; midtrochanter unmodified; mid- and hindcoxae inner margins broadly rounded. *Abdomen*: epipygium with well-developed subapical transverse ridge; hypopygium broadly triangular apically (Fig. 23). *Genitalia*: as in Figs. 25, 26. *Color* (Fig. 6): head yellow, except frons medially, mandibular apex and occiput black; thorax yellowish orange, except anterior face of pronotum medially black, scutum black between notauli surrounding large medial yellow spot, mesopleural venter and propodeal base black; legs orange to yellow except base of coxae blackish; mesopleural lamellae translucent with yellow or whitish

margins; abdominal segment I orange becoming yellow laterally; abdominal segment II yellow with narrow dark brown posterior band; abdominal segment III black; tergum IV yellow, basally and apically with narrow black band; terga V–VII yellow with narrow basal black band; sternum IV–VII black with yellow lateral spot; parameres yellow; wing membrane yellow-tinted, except marginal cell darker, brownish.

Female.—Unknown.

Type material.—Holotype ♂: Queensland, 30 km w Collinsville, 12 Sept. 1950, E. F. Riek (CANBERRA).

Etymology.—*orchros* = yellow; *tarsus* = legs, Greek, masculine.

Discussion.—Male *ochrotarsus* can be distinguished by the bright coloration, forefemur with basal depression and associated longitudinal carina and unmodified midfemur. The apically triangular hypopygium may or may not be diagnostic as the holotype is an old individual with highly worn mandibles and the hypopygial apex may also be worn.

***Leiothynnus spinigerus* Turner**
(Figs. 1, 8, 13, 15, 19, 26, 27)

Leiothynnus spinigerus Turner 1912:534. Lectotype male (designated by Kimsey & Brown 1993); Australia: Stradbroke Is., Moreton Bay (LONDON).

Male.—Body length 9–12 mm; punctuation as in *cardalae*. *Head*: flagellomere I 1.3–1.4× as long as broad; flagellomere II twice as long as broad; flagellomere III 2.4× as long as broad; punctuation as in *cardalae*. *Thorax*: mesopleuron with ventral part of scrobal sulcus obsolescent; forefemur with basoventral knob or swelling, separated from longitudinal carina by indentation (Fig. 13); forecoxa convex in cross section; midfemur with long basoventral tooth, nearly as long as tarsal claw; midtrochanter flattened adjacent to femoral tooth; mid and hindcoxae inner margins rounded. *Abdomen*: hypopygium

strongly exserted, parallel-sided, apex rounded with long medial tooth. *Genitalia*: as in Figs. 25, 26. *Color* (Fig. 8): black, with yellow and red markings; head black with yellow band along inner eye margin, clypeal apical margin yellow, antennal lobes yellow; scape and pedicel reddish; flagellum dark brown to black; pronotum with short transverse anterior yellow band, band sometimes ending at lateral notch; mesopleuron may have subalar yellow spot; scutellum in some specimens with small medial yellow spot; mesopleural lamella translucent with white or yellow margins; metanotum with yellow medial spot; meso- and metapleuron with small pale spot above coxae; coxae, trochanters and midfemoral base and hindfemur and hindtibia brown, rest of legs red; abdomen black except small lateral spot on tergum I-II or I-IV; wing membrane yellow-tinted, becoming brownish in marginal cell.

Female.—*Head* (Fig. 1): vertex dorsally convergent and angulate, not evenly rounded; gena evenly rounded, without sulci or grooves; posterior margin behind eyes strongly convex in front view; clypeus narrowly truncate apicomediaally; mandible slender, broadest basally, edentate. *Thorax* (Fig. 15): pronotal disk broad-

ly quadrate, with scattered erect setae of irregular lengths, particularly along anterior margin; propleuron with ventral tuft of long setae on either side; scutellum about as long as broad; propodeum with broadly convex dorsal surface, planar with scutellum, flattened posteriorly, parallel-sided in posterior view, with erect setae particularly laterally. *Abdomen*: tergum V apicomediaally emarginate; pygidium with lateral carinae parallel-sided or diverging medially, subtended laterally by short flange and long tuft of setae; sternum VI apex hoof-like (Fig. 19).

Material examined.—Australia: Qld, Stradbroke Is., Brisbane, Bundaberg, and Bribie Is.; 17 ♂♂ and 3 ♀♀ were examined including the lectotype.

Distribution.—Fig. 27.

Discussion.—The coloration of male *spinigerus* is similar to that of *mackayensis*, but without the broad yellow bands or stripes seen in that species. Other diagnostic features of male *spinigerus* are the unmodified foretrochanter, forefemur with basal knob and longitudinal carina, and long midfemoral tooth. Females have a distinctively narrowed vertex, tufted propleuron, and pygidium subtended by a short flange.

KEY TO MALES OF THE SPECIES *LEIOTHYNNUS*

- 1 Forefemur basoventrally convex, without depression or ridge 2
- Forefemur with basoventral depression, often accompanied by short longitudinal ridge (as in Figs. 12–14) 3
- 2 Midfemur with small basoventral angle (as in Fig. 11); flagellum monochrome, brown or red *linnis* Kimsey, new species
- Midfemur without basoventral angle; flagellum bicolored red and black (or dark brown) *cardalae* Kimsey, new species
- 3 Forefemur with distinct longitudinal basoventral ridge and associated depression (as in Fig. 12) 4
- Forefemur with basoventral cuplike depression without longitudinal ridge (as in Fig. 14) 5
- 4 Foretrochanter strongly concave or cuplike in cross-section (Fig. 12); forefemur without knob or swelling adjacent to longitudinal basal ridge (Fig. 12); midcoxa inner margin angulate and sharp-edged *ferricolus* Kimsey, new species
- Foretrochanter convex in cross-section, unmodified; forefemur with knob or swelling adjacent to longitudinal basal ridge (Fig. 13); midcoxa unmodified *spinigerus* Turner

- 5 Forefemur with large basoventral tooth, tooth nearly as long as tarsal claw; petiole (basal two abdominal segments) black; tarsi red *mackayensis* (Turner)
 - Forefemur with short basoventral tooth, less than half as long as tarsal claw, or basoventrally rounded without tooth or angle; petiole primarily yellow or orange; tarsi pale yellow, red or brown 6
 - 6 Midfemur unmodified; tarsi pale yellow *ochrotarsus* Kimsey, new species
 - Midfemur with small basoventral tooth or angle (Fig. 11); tarsi red to brown *multimaculatus* Kimsey, new species
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***Stethophotopsis*, a New Genus of Sphaerophthalmini (Mutillidae: Sphaerophthalminae) with a Brachypterous Male from Arizona**

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Abstract.—A new genus of Mutillidae from southern Arizona with an brachypterous male, *Stethophotopsis* Pitts, is described and illustrated, including the new species *Stethophotopsis maculata* Pitts. The genus can be distinguished from males of other sphaerophthalmine genera by the posterior position of the mesosternal processes, the dilated and elongated condition of the cuspis and the absence of plumose pubescence on the cuspis.

The subfamily Sphaerophthalminae includes approximately 71 genera in two tribes, Sphaerophthalmini and Dasylabrini. Dasylabrini are restricted to the Old World while Sphaerophthalmini occur in the New World, Japan, and in the Mediterranean and Australian regions (Brothers 1975). Of the 60 genera of Sphaerophthalmini, 55 occur in the New World. This tribe is distinguished by two synapomorphies apparent in both sexes: the approximately hemispherical, smooth and polished condition of the eye and the presence of plumose pubescence (Brothers 1975).

In a study of Mutillidae from the southwestern United States, two male specimens of an undescribed brachypterous species were found. Although no phylogenetic hypothesis is available for genera of Sphaerophthalminae, this new species is unique in several features considered to be of generic-level importance for the subfamily. This new genus and species are described, illustrated and discussed below.

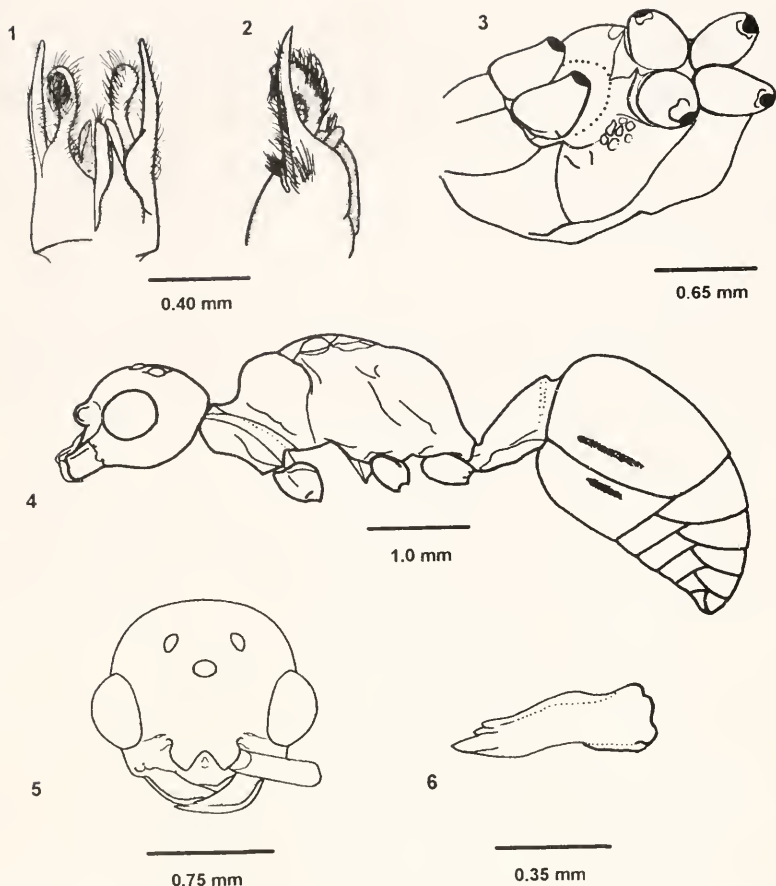
MATERIALS AND METHODS

We follow the terminology suggested by Menke (1993) for the scutum rather than that of Schuster (1958). The term "tibial spurs" is used instead of "calcaria."

We denote the second, third, etc. metasomal tergites as T2, T3, etc. and the second, third, etc. metasomal sternites as S2, S3, etc.

***Stethophotopsis* Pitts, new genus (Figs. 1–6)**

Male.—**Head:** As wide as thorax. Ocellular distance (Fig. 5) $2\times$ width of lateral ocellus. Clypeus forming a trapezoidal, truncated anterior lobe, slightly to moderately depressed below dorsal mandibular rim; clypeal base tuberculate. Malar space (Fig. 4) $0.5\times$ maximum eye width. Gena well developed, width approximately equal to width of mandibular base. Mandible tridentate apically, ventral margin with slight excision, not subtended by distinct sub-basal tooth. Antennal scrobes carinate above, with tubercle. First flagellomere $1.6\times$ length of pedicel; second flagellomere $1.3\times$ length of first flagellomere. Maxillary palp 6-segmented, labial palp 4-segmented. **Mesosoma:** Mesoscutum with notali present posteriorly, absent or obscure on anterior third of mesoscutum. Tegula glabrous. Wings brachypterous, reduced to $0.5\times$ length of tegula. Mesosternum (Fig. 3) armed with pair of densely pubescent, triangular tapering processes, originating near midline immediately anterior to me-



Figs. 1-6. *Stethophotopsis maculata*, Holotype. 1, Genitalia lateral view. 2, Genitalia, dorsal view on right, ventral view on left. 3, Sternum (legs except coxae, sculpture and pilosity omitted). 4, Body, lateral view (wings, legs except coxae, sculpture and pilosity omitted). 5, Head, frontal view (sculpture and pilosity omitted). 6, Left mandible.

socoxae, appearing to cup anterior margin of mesocoxae. Tibial spurs 1-2-2; tibiae slender, not flattened. *Metasoma*: First segment (Fig. 4) petiolate, slender, not nodose, moderately constricted dorsally and laterally at apex, distal width much less than that of base of segment 2. Segment 2 with both tergal and sternal felt lines. Apical margins of segments 1 and 2 with plumose pubescence. Pygidium short, subtruncate at apex. Hypopygium transverse, broader than long, laterally undefined. Paramere arcuate, stout at base and weakly dorsoventrally flattened. Cuspis (Figs. 1, 2) elongate, about equal

to free length of paramere, curved ventrally, basal portion cylindrical, distal portion dilated and weakly concave on ventral surface, ventral surface with dense simple pubescence distally. Digitus devoid of pubescence.

Female.—Unknown

Etymology.—From the Greek *stetho* "chest" + *photopsis*, a commonly used sphaerophthalmine suffix, referring to the characteristic sternal processes of this genus. Gender feminine.

Distribution.—USA, Southern Arizona.

Type species.—*Stethophotopsis maculata* sp. nov.

***Stethophotopsis maculata* Pitts, new species**
(Figs. 1–6)

Male.—*Length*: Holotype 7 mm, paratype 8 mm. *Color*: Head, thorax, petiole, second tergum, coxae, trochanters and tarsi brownish-yellow. Femora and tibiae dark brown. Third through seventh abdominal segments reddish-brown. Two round black maculations on anterior fourth of T2 with deep punctation, appearing raised above surrounding disk. Pubescence of head, pleural region, mesosternum and mesosomal sternites pale. Pubescence of thoracic dorsum golden-brown to pale. Pubescence of abdominal tergites pale except black in areas of tergal maculations. *Head*: Head as wide as thorax, rounded behind eyes in dorsal view. Ocelli salient, ocellular distance (Fig. 5) slightly greater than $2\times$ width of lateral ocellus, interocellar distance slightly greater than $2\times$ width of lateral ocellus. Clypeus anteriorly forming a trapezoidal, truncated anterior lobe, slightly to moderately depressed below dorsal mandibular rim. Malar space $0.5\times$ maximum width of eye. Gena (Fig. 4) well developed, width approximately equal to width of mandibular base. Mandible (Fig. 6) tridentate apically, ventrally with a slight excision not subtended by a distinct sub-basal tooth, with ventral carina ending before midlength and with complete dorsal carina, raised at midlength. Apical mandibular teeth with 1st tooth basal width $4\times$ and length $6\times$ the 3rd tooth; 2nd tooth basal width $1\times$ and length $2\times$ the 3rd tooth. Antennal scrobe carinate above, with small tubercle. First flagellomere $1.6\times$ length of pedicel; second flagellomere $1.3\times$ length of first flagellomere. Ridges of hypostomal region unmodified. Punctuation of vertex confluent. *Mesosoma*: Pronotum, scutum and scutellum shallowly, coarsely, confluent punctate. Scutum with subcomplete notauli, absent on anterior third of scutum. Tegula glabrous. Propodeum coarsely

punctate. Mesopleuron with oblique sulcus indistinct; sculpture reticulate throughout. Mesosternum (Fig. 3) armed with pair of triangular, tapering processes, originating immediately anterior to mesocoxae, situated slightly medially from center of coxae, covered with simple pubescence; sinus broadly U-shaped. Metasternum tridentate. Mesocoxae approximate and unarmed; metacoxa and trochanter unarmed. Wings brachypterous, reduced to 0.5 length of tegula. *Metasoma*: First segment (Fig. 4) petiolate, slender, not nodose, posteriorly moderately constricted dorsally and laterally, posterior width much less than base of second segment. T1 sparsely punctate, punctations separated by at least $2\times$ width. Anterior margin of T2 coarsely, confluent punctate becoming shallowly, sparsely punctate posteriorly; S2 moderately punctate, anterior fourth with median longitudinal carina; sternal felt line approximately $0.75\times$ length of tergal felt line. Posterior margin of T1 and T2 with plumose pubescence. Pygidium transverse, broader than long and subtruncate at apex. Hypopygium transverse, broader than long, laterally undefined by carinae. Paramere (Figs. 1, 2) arcuate, stout at base and little dorso-ventrally flattened, tapering, devoid of long setose pubescence. Cuspis elongate, reaching nearly to apex of paramere, outwardly curved, distal portion distinctly dilated and slightly spatulate, basal portion cylindrical; distal portion with dense, long simple pubescence, basal half sparsely and minutely pubescent. Digitus devoid of pubescence.

Female.—Unknown

Type material.—Holotype: "Brown Canyon, Baboquivari Mountains, Arizona, September 6, 1958, Stange and Menke" (LACM). Paratype: Arizona, Santa Cruz County, Madera Canyon, Santa Rita Mountains, 17–18.VIII.1949, Lloyd Martin (LACM).

Etymology.—From the Latin *maculata* "spotted," in reference to the pair of black

maculations on the anterior margin of the second tergite.

Comments.—The paratype closely resembles the holotype in most features except that it is slightly larger.

DISCUSSION

Stethophotopsis is a distinct genus in the Sphaerophthalmini (subtribe: Sphaerophthalmina). The unique sternal processes and the dilated, spatulate and elongate condition of the genitalic cuspis are apparently autapomorphic for the genus. *Stethophotopsis* will key to subfamily Sphaerophthalminae without difficulty in existing keys by Brothers (1993, 1995). In Schuster's (1958) key to the sphaerophthalmine males of the North American Southwest, *Stethophotopsis* fails to key beyond the first couplet, where it may be diagnosed by the autapomorphies listed above.

Lelej and Nemkov (1997) presented a phylogeny for the subfamilies of Mutillidae and synonymies for mutillid genera. Because this work remains controversial (Brothers 1999), we follow Schuster's (1958) classification of the sphaerophthalmine genera. The subfamilies recognized here are those presented by Brothers (1975, 1999). Currently, there is no phylogenetic hypothesis available for the subtribe Sphaerophthalmina. Although it is apparent that *Sphaerophthalma* is paraphyletic (pers. obs.), the other genera of Sphaerophthalmini may be monophyletic.

The new species described here cannot be placed in any of the established genera of Sphaerophthalmini because it differs from each one by characters considered to be of generic-level significance. In the discussion that follows, we distinguish *Stethophotopsis* from the related genera with which it is most likely to be confused.

Morsyma Fox, *Protphotopsis* Schuster and *Photomorphus* Viereck share some characters which are of taxonomic significance with *Stethophotopsis*, although they differ in genitalic morphologies and vari-

ous other diagnostic features. *Morsyma* is apterous and is superficially similar to *Stethophotopsis* because of its degree of brachyptery; however, *Morsyma*, has a broadly sessile abdomen, has smaller ovate eyes and lacks sternal processes, notali and a tooth on the antennal scrobe (Schuster 1958). *Protphotopsis* shares with *Stethophotopsis* a tridentate mandible and the lack of a ventral mandibular tooth, but it has the anterior pronotal margin distinctly emarginate, notauli absent, mesosternum unarmed and pubescence simple (Cambra and Quintero 1997). *Photomorphus* and *Stethophotopsis* have well developed sternal felt lines and a tuberculate clypeal base; however, *Photomorphus* has dentate ridges on the anterior margin of the mesosternum, has a ventral mandibular tooth, and either lacks or has only vestigial plumose pubescence (Schuster 1958).

Some subgenera of *Sphaerophthalma* Blake (*Sphaerophthalma*, *Physetapsis* and *Photopsioides*) and species of *Odontophotopsis* Viereck have a similar hypopygium morphology to that of *Stethophotopsis*. Also, some small individuals of *Sphaerophthalma* and *Odontophotopsis* are similar in having incomplete notauli. The mesosternum of *Sphaerophthalma*, however, is never modified with dentate ridges or processes. In *S. (Sphaerophthalma)* and *S. (Photopsioides)* the cuspis also is dilated; however, it bears plumose pubescence and is not spatulate. For *Odontophotopsis*, the cuspis is rod-like and the paramere is much longer than the cuspis. *Odontophotopsis (Odontophotopsis)* has small dentate processes situated on the mesosternal midline far removed from the mesocoxae and *O. (Periphotopsis)* has swollen, longitudinal processes running the length of the mesosternum.

Dilophotopsis Schuster and *Acrophotopsis* Schuster differ greatly from *Stethophotopsis* in having a large dilated sub-basal tooth on the mandibles, dorsoventrally flattened parameres and strongly depressed hypopygia with distinctly carinate lateral mar-

gins (Schuster 1958), all of which are lacking in *Stethophotopsis*.

Stethophotopsis shows the greatest apparent affinity to the genus *Acanthophotopsis* Schuster. These genera share the following characters: (1) the clypeus is truncate and depressed below mandibular rim, (2) the genitalic cuspis is flattened and dilated and (3) the mandibles are not dentate below but have a small excision (Schuster 1958). Despite these similarities, *Acanthophotopsis* differs in a number of important characters warranting separation, including the following: (1) loss of a mesotibial spur, (2) flattened and arcuate mesotibia, (3) cylindrical mesosternal processes arising anterior to the posterior margin of the mesosternum (whereas *Stethophotopsis* has triangulate ridges that arise from the posterior margin of the mesosternum and appear to cup the anterior margin of the mesocoxae), (4) complete notauli, (5) anteriorly reduced gena and (6) sternal felt line absent.

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New Genera of Angarosphecinae: *Cretosphecium* from Early Cretaceous of Mongolia and *Eosphecium* from Early Eocene of Canada (Hymenoptera: Sphecidae)

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Abstract.—The new genus *Cretosphecium* Pulawski and Rasnitsyn is described for two Early Cretaceous species from Mongolia: *C. lobatum* Pulawski and Rasnitsyn (type species) and *C. triste* Pulawski and Rasnitsyn. *Eosphecium* Pulawski and Rasnitsyn is described to include only the new species *E. naumanni* Brothers and Archibald from the Early Eocene of Canada. *Eosphecium*, tentatively assigned to Angarosphecinae Rasnitsyn, 1975, may represent the first Cenozoic record for the subfamily, known heretofore only from Early Cretaceous deposits.

Species of Angarosphecinae Rasnitsyn, 1975 (= Baissodinae Rasnitsyn, 1975) are early sphecid wasps that lack synapomorphies of the extant subfamilies. Only a small fraction of the available material has been described so far (Rasnitsyn 1975; Rasnitsyn et al. 1998, 1999), and three additional fossils that we attribute to this subfamily are described here. These specimens are characterized by a unique wing venation, found in no other sphecids, either fossil or extant; and one shows pronotal lobes, a unique synapomorphy of Apoidea. Two are from the Early Cretaceous, and the third is from the Early Eocene, the first record from the Cenozoic Era for the subfamily. Until now, Angarosphecinae (including much undescribed material housed at the Paleontological In-

stitute, Russian Academy of Sciences) were known exclusively from the Early Cretaceous.

Morphological terminology used here deviates from that of Brothers (1975) and Bohart and Menke (1976) in several ways and is as in Rasnitsyn et al. (1999). The following structures, variously termed in the literature, are here defined or redefined for the sake of clarity and convenience:

- adlateral line: parapsidal line of Bohart and Menke (1976); we prefer the term coined by Budrys and Kazenas (1992) as it is more informative (self-explanatory and analogous to the admedian line) and also because the term parapsidal line is used by many authors to designate the structure that Bohart and Menke and most other hymenopterists call notaulus;
- interpostgenal suture: line of fusion of the postgenae, extending from the oral cavity to the occipital foramen;

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- metasoma: abdomen excluding the propodeum (gaster of Bohart and Menke 1976);
- postgena: area between hypostomal carina and occipital foramen;
- spiracular lobe (Rasnitsyn 1988): pronotal lobe of Bohart and Menke (1976);
- costal space: cell C of Brothers (1975), costal cell of Bohart and Menke (1976);
- cell 1 + 2r: cell SC + R of Brothers (1975), submarginal cell I of Bohart and Menke (1976);
- cell 3r: cell R of Brothers (1975), marginal cell of Bohart and Menke (1976);
- cells 2rm and 3rm: cells 1S and 2S of Brothers (1975), submarginal cells II and III of Bohart and Menke (1976);
- cells 1mcu and 2mcu: cells S + M and 1M of Brothers (1975), discoidal cells I and II of Bohart and Menke (1976);
- cell 2cua: 1Cu of Brothers (1975), subdiscoidal cell of Bohart and Menke (1976);
- veins 2r-m and 3r-m: distal margins of cells 2rm and 3rm, respectively (as in Richards 1977, and Gauld and Bolton 1988), corresponding to crossveins 1s-m and 2s-m of Brothers (1975), and 1r-m and 2r-m of Bohart and Menke (1976); we consider the true 1r-m to be present only in primitive Symphyta such as the xyelid genus *Pleuroneura* Konow or *Xyela lata* D. Smith.
- veinlet 1r-rs: partial vein within cell 1 + 2r, originally separating cells 1r and 2r; called 1r by Bohart and Menke (1976).
- crossvein 2r-rs: vein separating cells 1 + 2r and 3r, called r-s by Brothers (1975) and 2r by Bohart and Menke (1976).

Figs. 1 and 2 are by APR and Fig. 3 is by DJB.

***Cretosphpecium* Pulawski and Rasnitsyn,
new genus
(Figs. 1, 2)**

Derivation of name.—*Cretosphpecium*, from the Latin word *creta* (chalk) and the Greek word *sphpekion* (little wasp); with reference

to its occurrence in the Cretaceous Period. Gender neuter.

Diagnosis.—*Cretosphpecium* has an unusually long cell 2rm whose posterior margin is longer than that of cell 1 + 2r, veins 1m-cu and 2m-cu are received by cells 2rm and 3rm, respectively, and cell 3r is truncate apically. A similar venation is found in *Eosphpecium*. In *Cretosphpecium*, however, vein 2r-rs is less than the height of pterostigma, cell 3r receives vein 3r-m next to the apical truncation, vein 1m-cu joins cell 2rm at the cell's midlength, cell 2rm is less than 3 times as long as high, and cells 2cua, 2mcu, and 1mcu are about equal in height. In *Eosphpecium*, vein 2r-rs is about equal to the height of pterostigma, vein 3r-m is markedly distant from the apex of cell 3r, vein 1m-cu joins cell 2rm before the cell's midlength, cell 2rm is almost 5 times as long as high, and cells 2cua and 2mcu are about twice as high as cell 1mcu.

Description.—The following complements the above characteristics. Pronotal hindmargin angulate dorsolaterally adjacent to spiracular lobe. Scutum: notaulus complete, extending from hindmargin to foremargin; adlateral line extending from hindmargin almost to foremargin. Forewing: vein 2r-m oblique, sinuous or straight, vein 3r-m oblique and sinuous (in *C. lobatum*, not preserved in *C. triste*), its anterior end insignificantly closer to wing margin than to apex of cell 3r; vein cu-a postfurcal. Hindwing (preserved only in *C. lobatum*): cu-a postfurcal, angled with first abscissa of Cu. Metasoma sessile.

Taxonomic position.—The presence of a spiracular lobe (visible in *C. lobatum*) demonstrates that *Cretosphpecium* is a member of Apoidea. The elongate notaulus that reaches the mesoscutal hindmargin is an ancestral character not found in any of the extant apoid genera but is typical of the subfamily Angarosphpecinae.

Type species.—*Cretosphpecium lobatum* Pulawski and Rasnitsyn, new species.

Composition.—Two species from the Early Cretaceous of Mongolia.

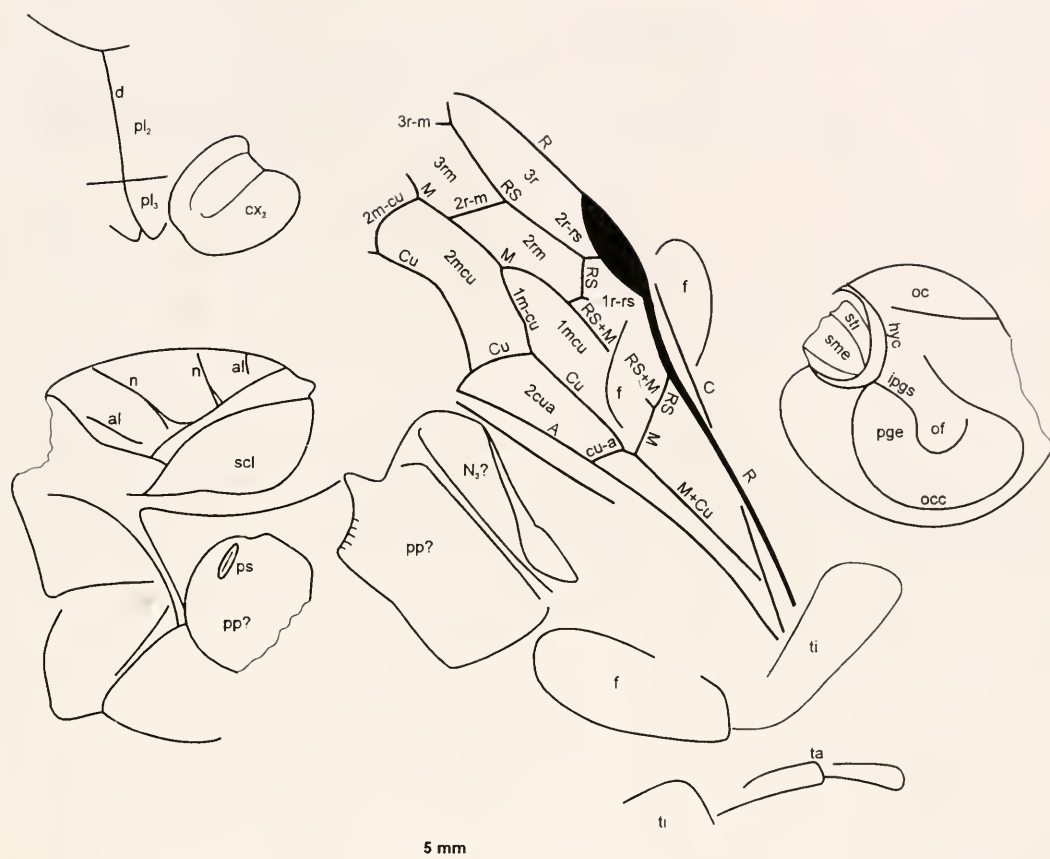


Fig. 2. *Cretosphegium triste* Pulawski and Rasnitsyn, new species; d: discrimin (interpleural suture); ipgs: interpostgenal suture; oc: eye; ps: propodeal spiracle. Other abbreviations as in Fig. 1.

Diagnosis.—Larger than *C. triste* (e.g., length of forewing about 9.0 mm rather than about 6.8 mm), vein 2r-rs emerging at about two-thirds pterostigmal length, vein 2r-m sinuous, and foremargin of cell 3rm shorter than height of cell.

Description.—Sex unknown. No coarse sculpture recognizable except pronotum transversely ridged. Head nearly circular, occipital carina complete, postgenae widely separated, gap between them obscured by bases of maxillae and labium. Mesoscutum with rudimentary median line. Metathoracic venter forming a subtriangular elevation between hindcoxae. Forewing: vein 2r-rs emerging at about two thirds of pterostigmal length; vein 2r-m sinuous, its fore end closer to 3r-m than to

2r-rs; vein 3r-m oblique, sinuous; maximum width of cell 3rm markedly less than its basal height. Length of midtrochanter more than twice width. Midbasitarsus longer than midtarsomeres II-IV combined, midtarsomere IV longer than wide. Metasomal segment I subtriangular, wider than long, hindmargin of sternum I shallowly emarginate. Sternum II longer and wider than I, its anterior margin straight. Apical sternum subtriangular, carinate laterally. Body length as preserved 16.2 mm, forewing about 9.0 mm long, head width 3.0 mm. Body dark (color unknown for missing parts: antennal flagellum, hindtibiae and tarsi), but the following are distinctly paler: midtarsus (except basitarsus base) and wing veins including pterostigma.

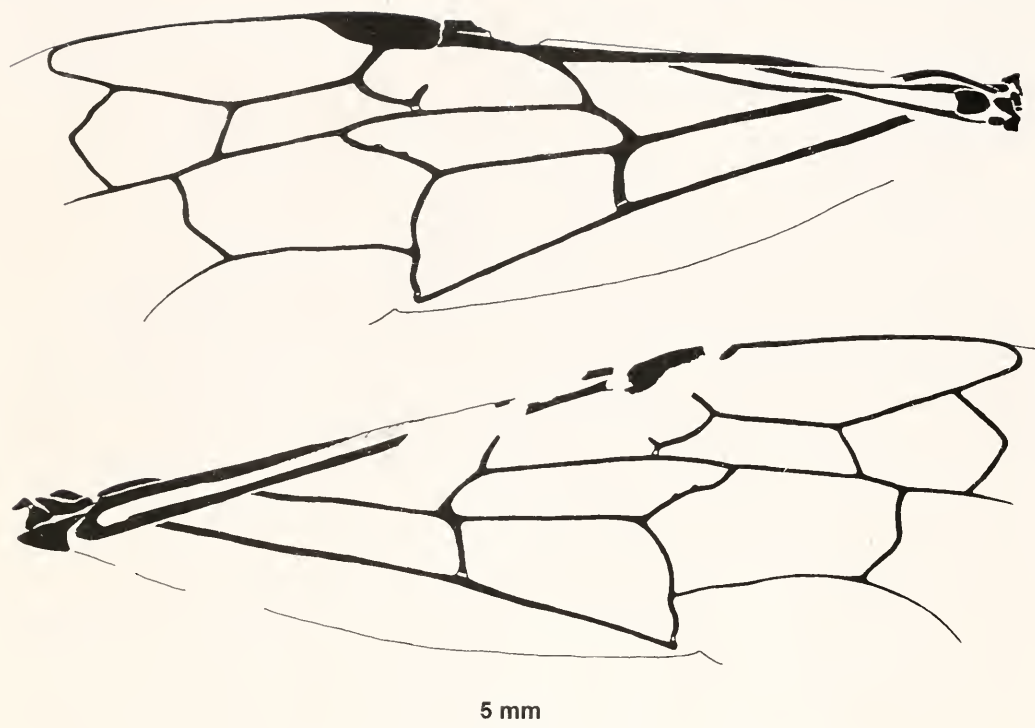


Fig. 3. *Eosphecium naumanni* Brothers and Archibald, new species.

Type material.—Holotype: Mongolia, Bayanhongor Aymag: Bon Tsagan, 5–8 km north of Bon Tsagan Nuur (= Bon Tsagan Lake); Early Cretaceous, impressed in marl of the Khurilt rock unit, Bon Tsagan Series (Sinitza 1993), possibly of Aptian age (Ponomarenko 1990). Deposited in the Paleontological Institute, Russian Academy of Sciences, Moscow, Russia (catalog number 3559/4533).

***Cretosphecium triste* Pulawski and Rasnitsyn, new species**
(Fig. 2)

Derivation of name.—*Triste*, Latin neuter adjective meaning sad; with reference to the specimen's poor preservation.

Diagnosis.—Smaller than *C. lobatum* (e.g., length of forewing about 6.8 mm rather than about 9.0 mm), vein 2r-rs emerging at pterostigmal midlength, vein

2r-m straight, and foremargin of cell 3rm longer than basal height of the cell.

Description.—Sex unknown. Head nearly circular, postgenae broadly contacting mesally, occipital carina complete and meeting hypostomal carina near midline of head. Scutum with no median line. Apex of metapleural venter with triangular emargination. Propodeal spiracle long, narrow. Forewing: vein 2r-rs emerging at pterostigmal midlength; vein 2r-m straight, its fore end equidistant from 2r-rs and 3r-m. Legs appearing thicker than in *C. lobatum*. Original color probably not preserved (entire specimen uniformly light).

Type material.—Holotype: Mongolia: Bayanhongor Aymag: Bon-Tsagan (other data as under *Cretosphecium lobatum* above). Deposited in the Paleontological Institute, Russian Academy of Sciences,

Moscow, Russia (catalog number 3559/694).

***Eosphecium* Pulawski and Rasnitsyn,
new genus
(Fig. 3)**

Derivation of name.—*Eosphecium*, from the Greek words *eos* (dawn, morning, early) and *sphekion* (little wasp); with reference to the Eocene age of the specimen. Gender neuter.

Type species.—*Eosphecium naumannii* Brothers and Archibald, new species.

Diagnosis.—Like *Cretosphecium*, *Eosphecium* is characterized by an elongate cell 2r_m (the length of its posterior margin is approximately equal to that of cell 1 + 2r), veins 1m-cu and 2m-cu are received by cells 2r_m and 3r_m, respectively, and cell 3r is truncate apically. Unlike in that genus, the length of vein 2r-rs in *Eosphecium* about equals the width of the pterostigma; the anterior end of vein 3r-m is removed from the apex of cell 3r by more than the height of cell 2r_m; veins RS + M and M (= posterior margins of cells 1 + 2r, 2r_m, and 3r_m) form an almost straight line (although *Cretosphecium lobatum* approaches this condition); vein 1m-cu joins cell 2r_m before the cell's midlength; cell 2r_m is almost 5 times as long as high (less than 3 times in *Cretosphecium*); and cells 2cu_a and 2m-cu are about twice as high as cell 1m-cu (about equal in *Cretosphecium*).

Taxonomic position.—In the absence of other evidence, we assign *Eosphecium* to Angarosphecinae based solely on the forewing venation pattern that resembles that of *Cretosphecium*. We also consider the above differences and the major difference in stratigraphic age sufficient to warrant its description a separate genus.

***Eosphecium naumannii* Brothers and
Archibald, new species
(Fig. 3)**

Derivation of name.—Named after Dr. Ken Naumann who collected the specimen.

Description.—The following characters are complementary to the generic diagnosis above: vein 2r-rs emerging at pterostigmal midlength; vein 2r-m straight, its fore end about equidistant from 2r-rs and 3r-m; vein 3r-m markedly angled near midlength; vein cu-a slightly postfurcal; vein Cu2 sinuous. Costal space densely setose towards apex and deeply pigmented (evident in counterpart), remainder of wing pale; veins dark. Forewing length about 14.2 mm (thus considerably larger than both species of *Cretosphecium*).

Type material.—Holotype (forewing only): Canada, British Columbia: Quilchena, 50°07'40.3"N, 120°30'34.7"W; Early Eocene: Coldwater beds of the Kamloops Group, 52–54 mya (Mathewes and Villeneuve in prep.). Deposited in the Department of Biology, Simon Fraser University, Burnaby, British Columbia, Canada, catalog number Q-0423a (part) and Q-0423b (counterpart).

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A New Species of *Nitela* (Hymenoptera: Sphecidae: Larrinae) from Australia with Notes on the Nests and Prey of Two Species

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Abstract.—*Nitela elegans* Matthews, a new species from Australia, is described and illustrated. The first biological data for *N. elegans* and *N. australiensis* Shultz, both nesting in pithy stems, are presented. Both prey on Psocoptera, and appear to progressively provision their cells. Prey of *N. elegans* were nymphs of sp. B (Psocidae) and nymphs of *Heterocaecilius* sp. (Pseudocaeciliidae). Prey of *N. australiensis* were nymphs of *Aaroniella rawlingsi* Smithers (Philotarsidae). There appear to be at least two generations per year in Canberra, Australia. The pteromalid chalcid *Eupelmophotismus pulcher* (Girault) was reared from pupae of both species. A clutch of 14 Ceraphronidae (?*Aphanogmus* sp.), possibly a hyperparasite of *E. pulcher*, was found inside a cocoon of *N. australiensis*.

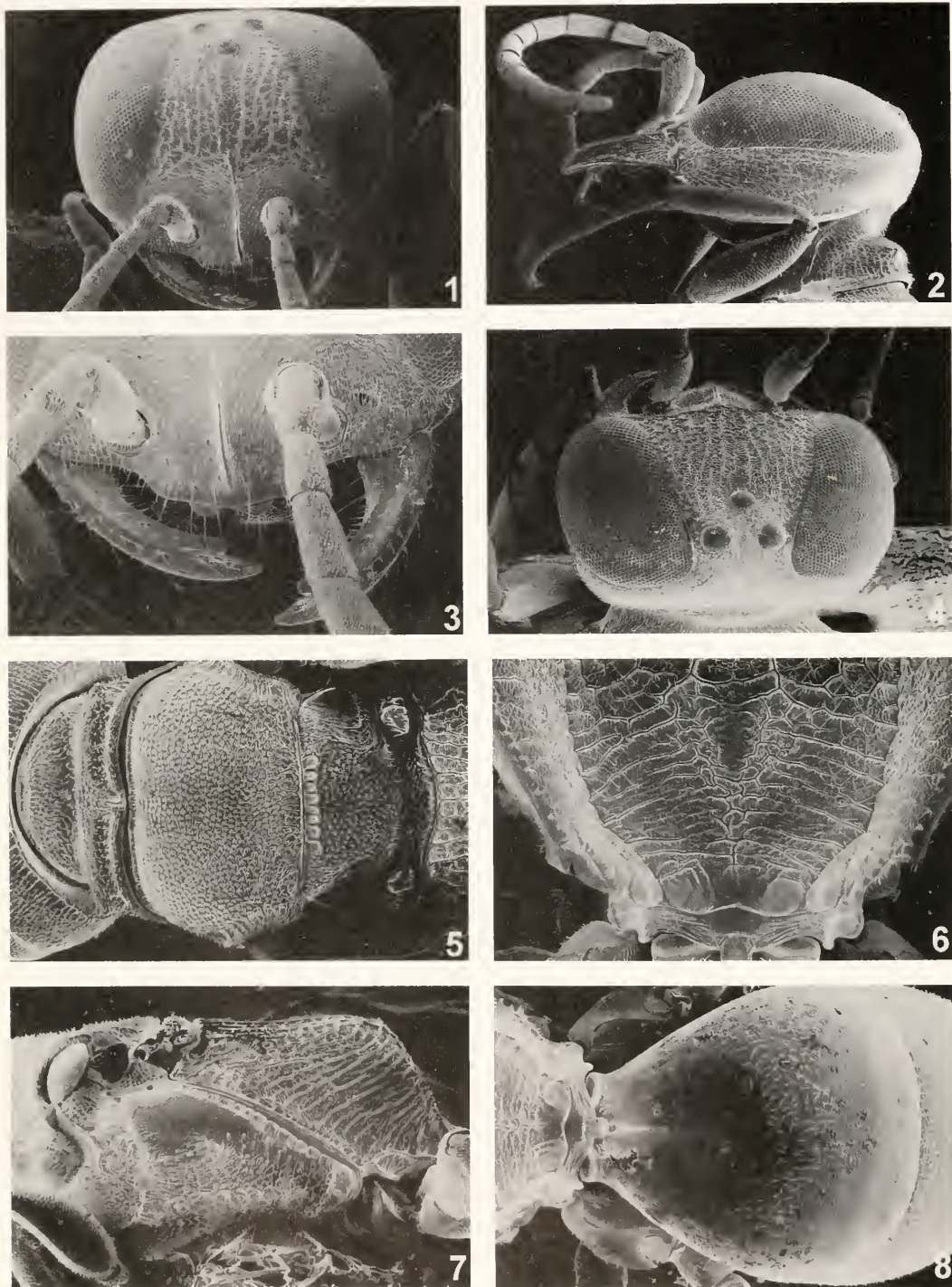
Although *Nitela* Latreille is found world-wide, with 43 species listed by Bohart and Menke (1975), only three species are described from Australia, and nothing has been published on the nesting behavior of any Australian species. Smithers (1990) recorded three species of Psocoptera as prey of an unidentified Australian species listed only as *Nitela* sp., but provided no nest details. Studies of other species of *Nitela* (Iwata 1939; Janvier 1962; Valkeila 1955), indicate that members of the genus nest in pre-existing cavities in stems, galls, and beetle burrows. Cells are separated from one another with bits of woody debris piled loosely in the burrow.

Material in the Australian National Insect Collection (ANIC) in Canberra suggests that there are several undescribed species of *Nitela* in Australia, but most are represented by only one or two specimens. In order to identify the two species discussed here, the types of each of the three named species were studied. Voucher specimens of the wasps, parasites, prey, and nests are deposited in the ANIC.

Nitela elegans Matthews, sp. nov. (Figs. 1–8)

Types.—Holotype female, 35.19S., 148.08E., Deakin, ACT, 4 April 1999, R. W. Matthews, deposited in ANIC. Paratypes: 4 females, same locality and collector data as holotype bearing dates 20.i.1999 (Bio Note 185), 23.i.1999 (one with label Bio Note 186), and 3.iii.1999, all deposited in ANIC.

Female.—**Head:** Globular, broader than high. Eyes strongly convergent dorsally, distance between eyes at level of the lateral ocelli about half distance between eyes measured just above the toruli. Frons (Fig. 1) evenly convex, rugulose, with longitudinal rugae more prominent. Vertex (Fig. 4) finely punctate, except space between lateral ocellus and orbit smooth; lateral ocelli separated by just less than their diameter, but narrowly separated from eye margin by about 0.25 their diameter. Gena (Fig. 2) finely rugulose at mandible bases, becoming faintly reticulate dorsally. Occipital carina entire, weakly costulate along anterior margin. Clypeus (Fig. 3) smooth, the apical margin rounded, very



Figs. 1-8. *Nitela elegans* Matthews, sp. nov., paratype female: 1, head, frontal view. 2, head and prothorax, lateral view. 3, clypeus, labrum, mandibles, frontal view. 4, head and pronotum, dorsal view. 5, mesoscutum and scutellum. 6, propodeum, dorsal view. 7, mesosoma, lateral view. 8, T1 dorsal view. Scale lines 0.1 mm.

slightly pointed medially, with prominent median longitudinal raised carina, evenly rounded in profile, not quite reaching clypeal margin. Labrum (Fig. 3) short, smooth broadly emarginate apically. Antennal scrobes (Fig. 1) faintly transversely microreticulate. Scape about twice as long as maximum breadth, length slightly less than length of pedicel plus first flagellar segment. Second flagellar segment $1.3\times$ as long as first. Mandibles (Fig. 3) bidentate, the inner tooth smaller, blunter, and shorter than apical tooth. *Mesosoma*: Transverse pronotal sulcus (Fig. 5) crenulate, slightly broader laterally, discontinuous medially where it is broken by a posteriorly projecting "V"; lateral margins of pronotum weakly angulate. Mesoscutum (Fig. 5) convex, uniformly punctate, except lateral margins crenulate. Scutellum uniformly punctate, separated from mesoscutum by narrow costulate furrow. Mesopleuron (Fig. 7) subalar area coriaceous; signum deep, area below it becoming coarsely punctate; episternaulus a distinct narrow crenulate furrow; hypersternaulus distinct, broader, crenulate to rugulose, fading posteriorly; area anterior to episternaulus rugose; propodeum lateral face longitudinally strigose with weak rugulose interspaces (Fig. 7); propodeal dorsal face rugulose with longitudinal rugae more prominent; propodeal hind face (Fig. 6) less strongly rugulose, with the transverse rugae more prominent. *Metasoma*: T1 (Fig. 8) more or less smooth and shining, very faintly coriaceous dorsally, with faint transverse microreticulation towards apical margin. T2-T6 with faint transverse microreticulation. *Forewing*: Length 3.0 mm. Marginal cell distally truncate, weakly appendiculate. 1r-m vein straight, interstitial with recurrent vein, and interrupted at about 0.25 of its length. *Color*: Head, mesosoma, metasoma non-metallic black. Antennae black. Mandibles black basally, lighter apically. Legs orange, except coxae black, femora suffused with brown, and distal three tarsomeres brown to black.

Wings hyaline, veins brown. *Body Length*: 5.0 mm.

Male: Unknown.

Notes.—In Turner's (1916) key this species runs to *N. kurandae* Turner. It differs in that the frons sculpture (Figs. 1, 4) is much more rugose, and the scapes and basal half of the flagellum are entirely black.

Biology.—Two active nests of this species were found in slender (ca. 5 mm diameter) pithy stems of an unknown dead plant (possibly *Lantana* sp.) on 20 and 23 January 1999 in a suburban yard of Deakin, ACT. One nest was newly initiated and the other nearly complete. The newly initiated nest was in a burrow 102 mm long and 2.0 mm in diameter. This nest contained a single half grown larva about midway along the burrow and 8 Psocoptera nymphs (sp. B, Psocidae). Two prey were adhering to the larva's body, and the others were scattered along the burrow. Those not yet fed upon were only lightly paralyzed, able to kick their legs and move their antennae, but lacked coordination. The female was resting near the entrance, head facing out. No nest structure was evident; there was no preliminary plug or cell closure.

The second nest's burrow was 136 mm long and 2.0 mm in diameter. It contained three completed cells and a fourth partially provisioned. The stem appeared previously to have been used by another wasp as the basal 36 mm of the burrow was tightly packed with pith fragments and old insect parts. Cell 1 was 12 mm long and contained a *Nitela* cocoon snug against the packed matter in the inner end of the burrow. The cylindrical tan-colored cocoon was 5 mm long and 1.8 mm in diameter. It was later found to contain a fully formed dead adult chalcidoid parasitoid, *Eupelmophotismus pulcher* (Girault) (Pteromalidae: Cleonyminae). Cell 2 was 8 mm long and contained fragments of an old cocoon. Cell 3 was 13 mm long and contained a mature larva spinning a ma-

trix of silk. Several faecal pellets adhered to the larva's body. Cell 4 was incomplete and contained 2 prey, both nymphs of *Heterocaecilius* sp. (Pseudocaeciliidae). No egg was present and both prey were lightly paralyzed and able readily to move their appendages. Beyond these prey the female was resting facing out.

The cells were separated by partitions consisting of numerous bits and pieces of organic debris, mostly not identifiable, but appearing to be small bits of bark, pith, insect exoskeleton fragments, seeds, husks, caterpillar faeces, etc. loosely packed along the burrow. The lengths of the partitions closing the three cells were 7 mm, 33 mm, and 2 mm long respectively. That cells 1 and 2 may have belonged to an older, prior nest is suggested by the fact that the cocoon in cell 2 was old and empty, the cocoon in cell one contained a dead parasite, and the closing plug of cell 2 was very long.

Both nests contained incomplete cells apparently being actively provisioned by the respective females. The first contained a partly grown larva in the cell and the second did not yet have an egg. Taken together, these facts suggest that either delayed mass provisioning or progressive provisioning is practiced in this species. Regardless, it appears that cells are not closed until the larva is essentially full grown.

The two prey species are typically found either on bark, branches, and twigs, or on the undersides of green leaves (C. N. Smithers, *in litt.*). Nine prey found in another nest (presumed to be *N. elegans*) were also identified as psocid sp. B.

The parasitoid genus *Eupelmophotismus* with about eight known species (Nauermann, unpublished) is endemic to Australia and New Guinea. Previous hosts recorded for *E. pulcher* are bees, including *Hylaeus* sp., *Amphylaeus morosus* (Smith), (both Colletidae) and *Neoceratina australensis* Perkins (Anthophoridae) (Boucek 1988), and the sphecoid wasp, *Psenulus in-*

terstitialis Cameron (Matthews 2000). All of these hosts are twig nesters like *N. elegans*. Presumably *E. pulcher* oviposits through the stem wall and attacks the pupal stages of its host, although it is possible in the case of *Nitela* that it burrows through the loose cell partitions to reach its host.

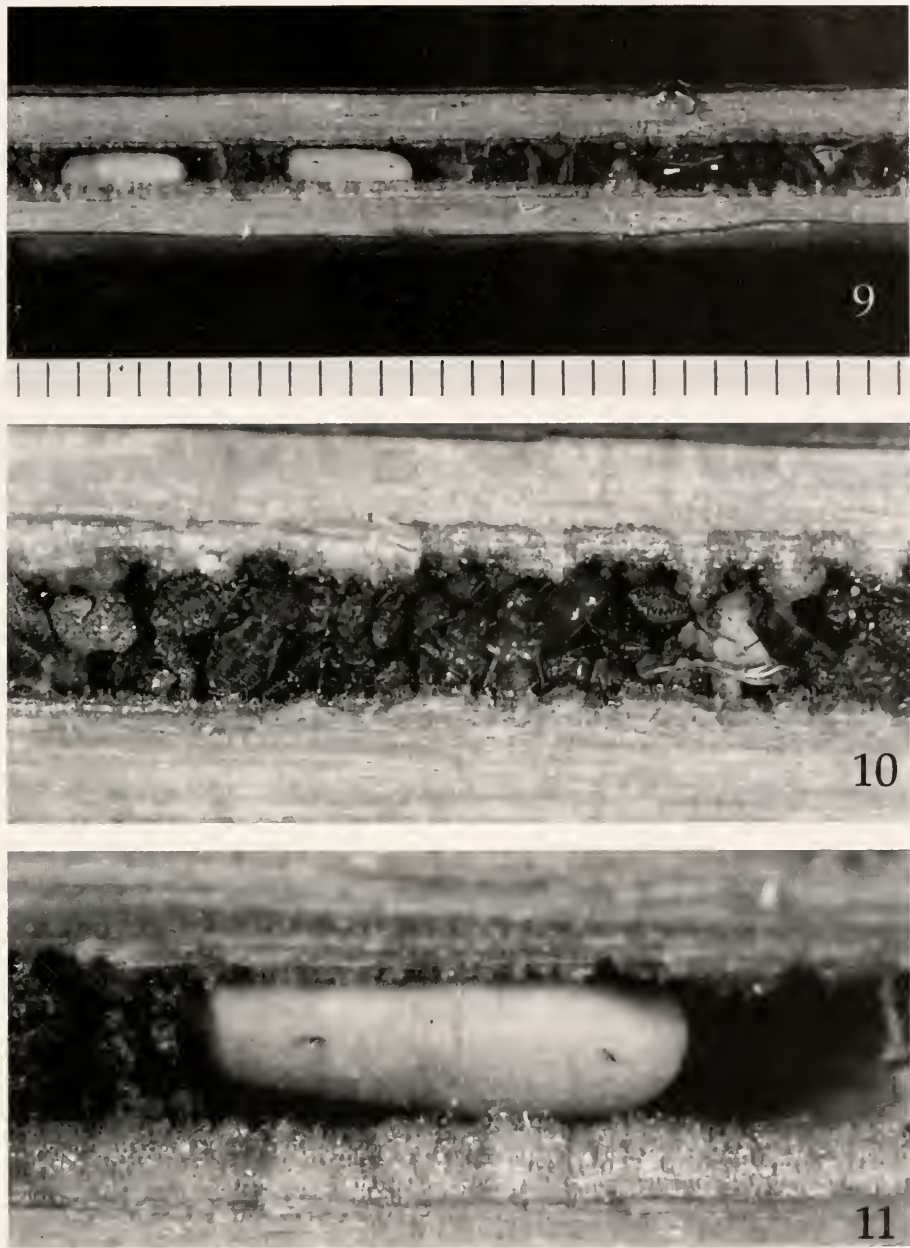
Nitela australiensis Schulz

This entirely black species of *Nitela* is widespread throughout Australia, although it has not yet been recorded from the Northern Territory.

Biology.—Turner (1916) speculated that it nested in old beetle burrows in dead eucalypts. I encountered it nesting in pithy stems of various unidentified plants in Deakin, a suburb of Canberra, ACT. Contents of three nests discovered from 31 January to 4 March 1999 are reported here.

Architecturally the nests were indistinguishable from those of *N. elegans*, being in burrows which had been excavated in slender (ca. 5–7 mm diameter) pithy stems, ranging from 27 to 96 mm long and 2 mm in diameter. From one to five cells were separated by loose aggregations of bits of organic debris, and were indistinguishable from those of *N. elegans*.

Two nests were complete when collected on 31 January 1999. One contained 5 cells, each with a typical tan-colored *Nitela* cocoon. On 27 February a single chalcid parasite (*Eupelmophotismus pulcher*) and three *N. australiensis* females were found to have emerged. One additional emerged wasp escaped. The second completed nest apparently consisted of two cells. Cell 1 contained a tan-colored *Nitela* cocoon 5.2 × 1.5 mm at the base of a short 27 mm long burrow. When later checked this cocoon was found to be moldy. One dead female adult was found among the closure debris which more or less filled the outer 20 mm of the burrow. It is likely that she had recently emerged from a second cell which had been destroyed in the process



Figs. 9–11. *Nitela australiensis* Schulz: 9, Portion of nest showing two cocoons, a mature larva, and prey separated by partitions of various lengths (scale marks are mm); 10, closeup of the 20 *Aaroniella rawlingsi* prey packed tightly in the cell; 11, cocoon, closeup, and the silk parchment-like inner lining on the partition at right, plus bits of the particles that separated the cells. Scale in 10 & 11 is the same, the cocoon is 4 mm long.

since there were *Nitela* cocoon fragments mixed among the closure particles.

The third nest (Fig. 9) collected on 4 March 1999 was incomplete and a female

was found resting in the burrow. This nest, in a burrow 74 mm long and 2 mm in diameter, contained four completed cells and a fifth cell (Fig. 10) containing 20

moribund psocid nymphs packed tightly together, one with an egg attached. The egg was on one of the innermost prey affixed obliquely across the venter of the prey's thorax. It measured 1.2 by 0.3 mm. Although laid on one of the first prey items, the egg had not yet hatched. However, the larva in the preceding cell was already spinning, having consumed all the prey. This suggests that new cells are not provisioned until the larva in the previous cell is nearly full grown.

Prey were all nymphs of *Aaroniella rawlingsi* Smithers (Philotarsidae), a bark dwelling species. The delicate tan-colored cocoons (Fig. 11) in cells 1–3 all contained diapausing prepupae and were 4.0–4.5 mm long. The mature spinning larva in cell four was later found dead. Each completed cell had a thin silk or parchment-like inner closing partition to which pieces of the particles separating the cells were attached. These partitions appear to have been constructed by the mature larva during the process of forming its cocoon. Such a partition, which was always constructed in the base of the cell, may help the larva to know the proper orientation for its cocoon.

Another nest, apparently belonging to this species, was collected on 31 January 1999. It had been usurped by another cavity-nesting wasp, *Arpactophilus* sp. (Sphecidae: Pemphredoninae). The basal 33 mm of the burrow contained 4 cells with cocoons, from three of which emergence had taken place. The fourth cocoon, still intact, was opened to reveal a clutch of 14 adult ceraphronid parasites (?*Aphanogmus* sp.), probably hyperparasites of *E. pulcher*. Also present in the nest debris was a single dead *N. australiensis* female.

In the Australian National Insect Collection is a series of *N. australiensis* reared on 21 Feb. 1986 from a trap nest from Nadgee Nature Reserve, New South Wales by E. A. Sugden. This artificial burrow was 60 mm long and had a bore diameter of 4.5 mm. It contained six cells separated by

coarse sawdust particles, bits of charcoal, bits of a blackish resinous substance, and small bits of frass. From this nest three females and two males had been reared (E.A. Sugden, personal communication).

It appears that there are at least two generations per year in the Canberra area. Evidence is circumstantial, based on the fact that progeny from the nest collected in late January emerged by late February, whereas progeny of the nest collected in early March had entered diapause.

DISCUSSION

The identity of the *Nitela* species mentioned by Smithers (1990) remains unknown. Associated specimens were not found in the collection of the Australian Museum. However, except for a single female of *Peripsocus milleri* (Tillyard) (Peripsocidae), the prey used by this species were all nymphs belonging to the Elipsocidae and Caeciliidae. Thus the Australian species of *Nitela*, like their congeners elsewhere in the world, specialize on Psocoptera (but see Zuijlen (1994) who notes a possible record for Zoraptera for *N. bifida* Menke from Costa Rica), primarily those groups that live on the surface of bark, with a strong preference for nymphs. Six families of psocids (Caeciliidae, Elipsocidae, Peripsocidae, Philotarsidae, Pseudocaeciliidae, and Psocidae) have now been recorded as prey of Australian *Nitela*.

The provisioning data also suggest that parental investment by the female is rather extensive. Probably either progressive provisioning or delayed mass provisioning is normal in both species. At the very least, the female appears to wait to begin a new cell until the larva in the previous cell is nearly full grown. Interestingly, the two parasitoids reared from these species were both found inside the cocoon. Because parental care apparently ceases by the time the larva is full grown, perhaps it is not surprising that the cocoon stage would be the most vulnerable to parasitism.

The only record of a nest of *Nitela* from southern Africa concerns an undescribed entirely black species, 4.6 mm in length (Fred and Sarah Gess, unpublished). It was constructed in a trap nest placed vertically among dry inflorescence stems of *Berkheya* (Asteraceae) on a stream bank in the Goegap Nature Reserve, Springbok, Namaqualand in low karroid scrub. Collected on 21 October 1987, the nest burrow was 288 mm long and 6.5 mm diameter. The nest burrow was closed at both ends, with a crescent-shaped entrance at mid-length. The nest had been in the field for six days when collected, and was found to have two completed cells provisioned with unidentified Psocoptera and closed with dry plant detritus and seeds. In neither cell were all the prey consumed before the larva spun a creamy-white cocoon with dense brittle walls 0.06 mm thick and rounded at both ends. A female later emerged from a cocoon that was 5.2 mm long and 2.0 mm diameter. The other cocoon (not measured) produced a male.

ACKNOWLEDGEMENTS

I thank Dr. C. N. Smithers (Sydney Museum) for identifying the Psocoptera prey, and Dr. Gary A. Gibson (Canadian National Collection, Ottawa, Canada) for identifying the chalcid parasite. Dr. Ian D. Naumann (CSIRO Entomology) provided valuable advice and assisted in identifying the *Nitela* species and the ?*Aphanogmus* sp. Fred and Sarah Gess kindly shared unpublished notes on a South African species of *Nitela*, and their review of the manuscript greatly improved it. Holotypes of *Nitela* species were kindly

loaned from the British Museum of Natural History (London) and the Museum für Naturkunde, Humboldt Universität (Berlin) by Ms. Christine Thompson and Dr. F. Koch, respectively. Eric Hines (CSIRO) helped with the SEM photographs and the nest and prey photos were taken by David McClenaghan (CSIRO). Financial support from the University of Georgia and a McMaster Fellowship from CSIRO are gratefully acknowledged.

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New Synonyms in Central and South Asian Sphecidae (Hymenoptera)

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Abstract.—A study of type material at the Natural History Museum, London, England, revealed 9 new synonyms for species described from Central Asia and former British India. These names are: *Ammophila bolanica* Nurse, 1903 = *Podalonia hirsuta mervensis* (Radoszkowski, 1887); *Cerceris nursei* Turner, 1912 = *Cerceris antennata* F. Morawitz, 1890; *Cerceris supposita* Kohl, 1916 = *Cerceris rothneyi* Cameron, 1890; *Cerceris compta* Turner, 1912 = *Cerceris turkestanica* Radoszkowski, 1893 (= *Cerceris rufonodis* Radoszkowski, 1877); *Cerceris barrei* Radoszkowski, 1893 = *Cerceris tetradonta* Cameron, 1890; *Cerceris rhynchophora* Turner, 1912 = *Cerceris unidentata* F. Morawitz, 1890; *Laphyragogus turanicus* Gussakovskij, 1952 = *Laphyragogus kohlii* (Bingham, 1896) (described in *Lianthrena*); *Palarus nursei* Turner, 1911 = *Palarus funerarius* F. Morawitz, 1890; and *Philanthus marikovskii* Kazenas, 1977 = *Philanthus elegantissimus* Dalla Torre, 1897 (= *Philanthus elegans* F. Smith, 1873). Lectotypes are designated for *Ammophila bolanica*, *Cerceris compta*, *Cerceris nursei*, *Cerceris rhynchophora*, *Laphyragogus kohlii*, *Laphyragogus turanicus*, and *Palarus nursei*.

One major problem facing students of Central Asian insects is their relation to the biotas of Pakistan and northwestern India. For a variety of reasons, Russian authors who studied the sphecids fauna of Central Asia over the last 140 years (Eversmann, Radoszkowski, F. Morawitz, Shestakov, Gussakovskij, Marshakov, myself and others) have not considered the species described from former British India (now India and Pakistan) by Cameron, Bingham, Nurse, F. Smith, and Turner. These latter authors, conversely, showed little interest in the work of Russian authors. The two areas, however, are not only adjacent geographically, but they closely resemble each other in their habitat types and ecological conditions (ranging from lowland hot deserts to high mountains with glaciers). With hundreds of species described on each side, it is inevitable that the ratio of synonyms may be high. A number of synonyms in Sphecidae were established by Pulawski (1975, 1979, 1995),

Marshakov (1977), Budrys (unpublished), and Antropov (unpublished).

For more than 25 years I have been studying sphecids wasps of Kazakhstan and adjacent republics of Central Asia. I previously studied almost all the types of the species described by earlier Russian authors during my many visits to the Zoological Institute of Russian Academy of Sciences in St. Petersburg, and to the Zoological Museum of Moscow State University (Moscow, Russia). It was therefore important to compare these types with types of the species described by British authors.

The Museum of Comparative Zoology at the Harvard University (Cambridge, Massachusetts, U.S.A.) awarded me an Ernst Mayr grant for the travel to the Natural History Museum in London and to the University Museum of Natural History in Oxford to study these types. I worked there for 6 weeks in August and September 1997. I have studied nearly 200 types and found nine new synonyms.

The following abbreviations are used in the text to designate institutions where the type material is housed:

- KRAKÓW: Instytut Systematyki i Ewolucji Zwierząt, Polska Akademia Nauk, Kraków, Poland.
 NHML: The Natural History Museum, London, Great Britain.
 OXUM: University Museum of Natural History, Oxford University, Great Britain.
 ZIN: Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia.
 ZMMU: Zoological Museum, Moscow State University, Moscow, Russia.

LIST OF SPECIES

(arranged alphabetically by their valid names)

Cerceris antennata F. Morawitz

Cerceris antennata F. Morawitz, 1890:598, ♂. Holotype: ♂, Turkmenistan: Küren-Dagh (ZIN, examined).

Cerceris nursei Turner, 1912:512, ♀, ♂. Lectotype: ♂, Pakistan: Quetta (NHML, examined), present designation, in order to ensure that the name is properly and consistently applied. **New synonym.**

The lectotype of *C. nursei* bears the following labels: 1. Quetta 5.03, 2. *Cerceris nursei* Turn., type ♂, and 3. Nurse Coll.: 1915-34.

This species belongs to the *specularis* group. It differs from closely related species by the markedly concave clypeus, unusually short pygidial plate, and presence of flat brushes of dense setae in posterolateral corners of male sternum VI (Kazenas 1984:201-203).

Cerceris rothneyi Cameron

Cerceris rothneyi Cameron, 1890:251, ♀ (as *Rothneyi*, incorrect original capitalization). Lectotype: ♀, India: West Bengal: Barrackpore (OXUM), designated by Empey, 1984:79 (Article 74.6).

Cerceris supposita Kohl, 1916:122, ♂. Syntypes: Turkmenistan: Serakhs (KRAKÓW, examined). **New synonym.**

The lectotype of *Cerceris rothneyi* should be in Oxford (Empey, 1984), but I was unable to locate it. However, 3 specimens (2 ♀, 1 ♂) in NHML agree with the original description. The first specimen has the following labels: 1. N. Kanara, and 2. *Cerceris rothneyi* Cam.; the second one: 1. N. Kanara, and 2. Bombay Presidency, pres. by E. Comber 1910-255; the third one: 1. T.R. Bell, Karachi, 2. *Cerceris rothneyi* Cam. ♂, and 3. 1911-276.

I consider these specimens to be conspecific with *C. supposita* Kohl, a member of the *bupresticida* group. It differs from all closely related species by the combination of the clypeal structure in the female, form of the vertical lamella on female sternum V, sculpture of propodeal enclosure, color, and other features (Kazenas 1984:79-81). In particular, the clypeal free margin of the female has 4 teeth; the vertical lamella of sternum V has a roundly prominent margin; the propodeal enclosure is fully unsculptured, shiny; the female pygidial plate is not narrowing posterad; male tergum VI and sternum VI each has a posterolateral tooth. Also, tergum I is partly red (also tergum II in some specimens), whereas female tergum IV has an uninterrupted pale yellow fascia apically.

Cerceris tetradonta Cameron

Cerceris tetradonta Cameron, 1890:261, ♀, ♂. Syntypes: N. India: Poona (depository unknown).

Cerceris barrei Radoszkowski, 1893:68, ♀, ♂. Syntypes: Turkmenistan: Serax (KRAKÓW, not examined). **New synonym.**

There are six specimens of *C. tetradonta* Cameron in NHML; one of them was collected in Pakistan (Karachi), three came from India (Abu, Deesa, and Khandala), and two from Sri Lanka. They are conspecific with specimens of *Cerceris barrei* Radoszkowski from Turkmenistan in ZIN

determined by Gussakovskij and Shestakov. *C. tetradonta* belongs to the *albofasciata* group and closely resembles *C. albofasciata* Rossi, but differs by the form of the clypeal free margin in the female and details of the body sculpture and color (Kazenas 1984:185–186). In particular, the clypeal free margin is conspicuously dentate, the mesopleuron and propodeal side have yellow spots, and the gastral sterna largely and the legs are yellow.

Cerceris turkestanica Radoszkowski

Cerceris rufonodis Radoszkowski, 1877:56, ♀, ♂. Syntypes: Uzbekistan: Djisak, Tashkent; and Kyrgyzstan: Osh in Fergana Valley (ZMMU, examined). Preoccupied by *Cerceris rufinodis* F. Smith, 1856 (Article 58.12, use of different connecting vowel).

Cerceris turkestanica Radoszkowski, 1893:66. Replacement name for *Cerceris rufonodis* Radoszkowski, 1877 (proposed to replace *Cerceris rufinoda* Cresson, 1865).

Cerceris compta Turner, 1912:803, ♀. Lectotype ♀: Pakistan: Karachi (NHML, examined), present designation, in order to ensure that the name is properly and consistently applied. **New synonym.**

The lectotype female in NHML has the following labels: 1. Type, 2. E. Comber, Karachi, Oct. 09, 3. *Cerceris compta* Turn. Type, 4. Bombay Presidency, pres. by E. Comber 1910-255, and 5. B.M. Type Hym. 21.1, 362.

The type of *C. compta* is identical with *C. turkestanica*. This species, a member of the *rybyensis* group, is characterized by the form of the female clypeus whose free margin is slightly sinuous on each side of the small, median incision. Also, sternum II has a prominent basal plate, the propodeal enclosure is almost entirely smooth, and the gastral color pattern is distinctive (see Kazenas, 1984:35); gastral segment I may be red or black. The propodeal side has a large yellow spot, and the legs are yellow except the femora are black ventrally.

Cerceris unidentata F. Morawitz

Cerceris unidentata F. Morawitz, 1890:601, ♀. Holotype: ♀, Turkmenistan: Kopet-Dagh near Chuli (ZIN, examined).

Cerceris rhynchophora Turner, 1912:510, ♀, ♂. Lectotype: ♀, Pakistan: Quetta (NHML, examined), present designation, in order to ensure that the name is properly and consistently applied. **New synonym.**

The lectotype female of *C. rhynchophora* in NHML has the following labels: 1. Type H.T., 2. Quetta 5.03, 3. *Cerceris rhynchophora* Turn., Type, 4. ♀, and 5. B.M. Type Hym. 21.1.426.

The specimens of *C. unidentata* F. Morawitz from Turkmenistan in ZIN are conspecific with the lectotype female of *C. rhynchophora* Turner. The species differs from other *Cerceris* by the following: propodeal enclosure closely punctate and with fine, transverse ridges; jugal lobe of hindwing 7–9 times shorter than anal cell; middle clypeal lobe in female with characteristic, overhanging, roof-like projection, in male with narrow, longitudinal carina and tridentate free margin (see Kazenas, 1984:178–180).

Laphyragogus kohlii (Bingham)

Lianthrena kohlii Bingham, 1896:213, ♀, ♂. Lectotype ♂: "N. India", may be Pakistan: Punjab: no specific locality (NHML, examined), present designation, in order to ensure that the name is properly and consistently applied.

Laphyragogus turanicus Gussakovskij, 1952:227. Lectotype: ♀, Tajikistan: Ayvadj at Kafirngan River (ZIN, examined), present designation, in order to ensure that the name is properly and consistently applied. **New synonym.**

There are 3 specimens in NHML. Of them, 1 ♀ and 1 ♂ were collected in Deesa and 1 ♂ (lectotype) is simply labeled North India. The last specimen has the following labels: 1. Type, 2. N. Ind., 3. *Lianthrena kohlii* Bingham. ♀ Type, and 4. B.M. Type 21.88. It is actually a male.

De Beaumont (1959) and Gussakovskij

(1952) discussed color differences between *kohlui* and *turanicus*. The specimens I studied do not differ morphologically and are very similar in color, so I consider them conspecific. The species differs from its congeners by the form of the first metatarsal article in the female and the structure of the flagellum and sternum VII in the male (Gussakovskij 1952).

Palarus funerarius F. Morawitz

Palarus funerarius F. Morawitz, 1890:136, ♀. Holotype: ♀, Mongolia: Zagan-Buryuk (ZIN, examined).

Palarus nursei Turner, 1911:481, ♀, ♂. Lectotype: ♂: Pakistan: Quetta (NHML, examined), present designation, in order to ensure that the name is properly and consistently applied. **New synonym.**

There are 3 specimens (2 ♀, 1 ♂) of *P. nursei* in NHML. The lectotype male has the following labels: 1. Type H.T., 2. Quetta 6.03, 3. ♂, 4. *Palarus nursei* Turner Type, 5. Col. C.G. Nurse Collection 1920–72, and 6. B.M. Type Hym. 21.77.

The specimens of *P. nursei* from Quetta, Pakistan and of *P. funerarius* from many localities in Central Asia are very close morphologically and to my mind conspecific. The differences in color are not conspicuous. *P. funerarius* is similar to *P. bisignatus* F. Morawitz, but differs in color and in structure of the male flagellum (F. Morawitz 1890b:136–139). Also, male sternum I of *P. funerarius* has a pair of tubercles (none in *P. bisignatus*) and the apical prominence of sternum II has 2 transverse carinae (one in *P. bisignatus*, evanescent in some specimens). The gaster of *P. funerarius* has no red, and femora have a large black spot each.

Philanthus elegantissimus Dalla Torre

Philanthus elegans F. Smith, 1873:415, ♀. Holotype or syntypes: "N. India", may be Pakistan: no specific locality (depository unknown). Preoccupied by *Philanthus elegans* F. Smith, 1856, now in *Trachypus*.

Philanthus elegantissimus Dalla Torre, 1897:485.

Replacement name for *Philanthus elegans* F. Smith, 1873.

Philanthus marikovskii Kazenas, 1978:662, ♀, ♂. Holotype ♀: Kazakhstan: 15 km E Ayak-Kalkan (ZIN, examined). **New synonym.**

I was unable to locate the original specimens of F. Smith either in London or in Oxford, but 3 specimens in NHML (2 ♀ and 1 ♂) from Deesa probably collected by C.G. Nurse agree with the original description. I consider them to be conspecific with *Philanthus marikovskii*. The species is morphologically close to *Ph. venustus* (Rossi) and *Ph. rubriventris* Kazenas, but differs in having extensive pale yellow coloration (Kazenas 1978: 662–664).

Podalonia hirsuta mervensis (Radoszkowski)

Ammophila mervensis Radoszkowski, 1887:89, ♀, ♂. Syntypes: Turkmenistan: Samsaul; Caucasus; and Corsica (KRAKÓW, not examined).

Ammophila bolanica Nurse, 1903:8, ♀. Lectotype: ♀, Pakistan: Quetta (NHML, examined), present designation, in order to ensure that the name is properly and consistently applied. **New synonym.**

There are 3 ♀ of *A. bolanica* from Quetta in NHML. The lectotype has 6 labels: 1. Type, 2. Quetta, 3. ♀, 4. Type, 5. Coll. C.G. Nurse Collection 1920–72, and 6. B.M. Type Hym. 21730.

These specimens are conspecific with specimens of *A. mervensis* (Radoszkowski) from Transcaspia in ZIN and ZMMU. R.M. Bohart and A.S. Menke (1976) consider *A. mervensis* to be a subspecies of *Podalonia hirsuta* (Scopoli). It differs from the nominotypical subspecies in having an all black gaster.

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The Biology of *Thrincohalictus prognathus* (Perez) (Hymenoptera: Halictidae: Halictini)

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Abstract.—The Halictine bee *Thrincohalictus prognathus* (Perez) was studied in Israel in May and the beginning of June, 1998. Additional information was obtained from museum specimens. The species appears to be both common and widespread in northern Israel, particularly in the Galilee and Golan Heights where it occurs between altitudes of several hundred metres up to 1650m on Mount Hermon. Despite having an unusually elongate head, the species visits a wide range of flowers which generally do not possess a long corolla. Like most temperate halictines, only mated females overwinter and become active in the spring, as early as mid March. Males are found no earlier than mid May. The apparent age of females increases from March to May with newly eclosed, unworn individuals appearing in late May/early June. All worn early summer individuals were mated and had well developed ovaries. Thus, ovarian development and phenological data are inconsistent with the species being eusocial but are consistent with it being univoltine. The behaviour exhibited by paired females in artificial observation arenas indicates that *T. prognathus* possesses the repertoire of agonistic and cooperative behaviours usually found in halictines but that aggressive interactions predominate. Comparisons with other species indicate that the relative frequency of passing behaviour is very low and inconsistent with that expected for a communal species. I conclude that this species is probably solitary.

Phylogenetic methods are useful not only in determining polarity of evolutionary changes among character states, but also for predicting which species are particularly deserving of study (Packer 1997). Based upon phylogenetic data, the monotypic genus *Thrincohalictus* is thought to be particularly worthy of study because it appears to be the sister taxon to the well studied and behaviourally diverse genus *Halictus* (Eickwort et al. 1996; Packer 1997; Danforth et al. 1999). Thus, this species is particularly important for assessing the pattern of evolution of social behaviour in the bee tribe Halictini.

Thrincohalictus prognathus (Perez) is a relatively large, non-metallic halictine with apical bands of tomentum on the abdominal terga and, as the specific epithet suggests, a long face. It is known, from comparatively few specimens, to occur in

Turkey and northern Israel (Bluethgen 1955; Ebmer personal communication) at least as far south as Jerusalem where one male specimen is known from Mt. Scopus.

In May and June 1998 I studied this species in Israel. Although detailed sociobiological analysis requires observation over several months (if not years, Yanega 1988; Sakagami and Packer 1994), some suggestive information can be obtained from samples of dissected bees (Dunn et al. 1999). Additionally, behaviours of bees caught from flowers but forced to interact in artificial arenas (circle tubes) may also be suggestive of social or solitary behavioural ancestry (McConnell-Garner and Kukuk 1997; Wcislo 1997; Paxton et al. 1999; Packer, unpublished observations). In this paper I present data on i) the distribution of *T. prognathus* in Israel, ii) a list of the flowers that it visits, iii) data from

dissected and/or measured bees from all available samples and iv) the results of circle tube experiments. The last two sets of data are potentially useful in elucidating the type of social organisation *T. prognathus* might possess.

METHODS

Sampling and phenological assessment.—Most females of *T. prognathus* were collected with a hand net from flowers although some of the pinned specimens included in some analyses were swept from vegetation. Most males were collected while they flew rapidly over bushes or around small trees, presumably in search of females. Some females were pinned but most were preserved in buffered formalin (Pabalan 1998) for subsequent dissection, one was preserved in ethanol for DNA sequencing (Danforth et al. 1999). At two localities, a parking lot and adjacent roadside near a garbage dump near Hazor, and at the peak of Mount Meiron, both in the Upper Galilee, large numbers of females were observed, not all of them were collected. All males were pinned. Flower visitation data were obtained from field samples and, when given, also from pinned specimens.

Bees preserved in formalin were dissected to establish their degree of ovarian development and whether or not they had mated. The fraction of a fully developed oocyte found upon microscopic examination of each of the six ovarioles was estimated by eye. Whether the terminal oocyte was developing or being resorbed was noted. Resorbing oocytes have a fuzzy outline and are often misshapen (Goukon et al. 1988; Pabalan 1998). The spermathecae of inseminated females are opaque whereas those of unmated females are clear and appear like glass bowls.

Head widths of all females (museum specimens and those collected by the author) were measured to ascertain whether there was any seasonal size variation similar to that found in eusocial species in

which summer workers are generally smaller than spring gynes (Breed 1975; Packer and Knerer 1985). The number of nicks in one forewing margin was counted to estimate the relative age of specimens. The largest number of nicks counted was 24, consequently, bees with the entire margin slightly eroded were coded as 25 and those with more extensive abrasion coded as 30. Although in reality wing wear measures comparative levels of activity which will not always be directly related to age, it is of some utility. For example, completely unworn individuals will either have recently eclosed or be overwintered females at the early stages of nest initiation and heavily worn individuals will have been active foragers probably for several weeks or more.

Behavioural data.—Despite several days searching in one locality where the species was particularly common (in the vicinity of Hazor in the Upper Galilee), no nest sites were discovered. Behavioural observations were made upon pairs of bees interacting in a "circle tube"—a 20cm long piece of clear plastic with the ends joined together such that moving bees are forced to repeatedly interact with one another (Breed et al. 1978).

Methods generally followed those of earlier authors (Breed et al. 1978; McConnell-Garner and Kukuk 1997; Wcislo 1997b; Paxton et al. 1999; Pabalan et al. submitted) with the exception that bees were placed into circle tubes within ten minutes of capture. This was because it has been discovered that, for some halictines at least, ovarian resorption begins within 30 minutes of captivity (Pabalan 1998 and unpublished observations on *Lasiglossum zephyrum*), suggesting physiological changes are occurring which may be mirrored by altered behavioural interactions among females.

The range of behaviours noted within circle tubes were similar to those often found in other studies (see references above). Bees would sometimes nudge or

Table 1. List of flower records for *Thrincohalictus prognathus*.

Locality	# bees	Flowers
Females		
Mt. Hermon	8	<i>Nepeta cilicica</i> Labiatae
Neve Ativ	2	<i>Lonicera</i> sp. Caprifoliaceae
	3	<i>Phlomis chrisophylla</i> Labiatae
	1	<i>Cerasus prostrata</i> Rosaceae
Qiryat Shemona	1	<i>Papaver</i> Papaveraceae
Ein Fit	1	<i>Papaver</i> Papaveraceae
	1	<i>Onopordum blanchi</i>
Hazor	dozens	<i>Centaurea iberica</i> Asteraceae
	dozens	<i>Phlomis viscosa</i> Labiatae
El Rom	3	<i>Papaver</i> Papaveraceae
Mt. Meiron	dozens	<i>Silybum marianum</i> Asteraceae
Males		
Katzrin	1	<i>Echinops</i> Asteraceae
Snir	1	<i>Vitex angustastus</i> Verbenaceae
Ramot Naftali	1	<i>Ballota saxatilis</i> Labiatae

lunge at one another, back away from one another either with or without reversing or pass one another, venter to venter, a manoeuvre requiring coordination between individuals. A more aggressive behaviour, the C-posture was also observed. In this stance an individual bends its abdomen forward, beneath the thorax in an apparent attempt at stinging the individual in front of it. It has also been suggested that secretions from the Dufours gland may be released during this posture (Smith and Weller 1989). The occurrence of these behaviours was recorded continuously for 20 (one pair) or 30 (the remaining four pairs) minutes.

RESULTS

Flower records.—Table 1 shows the flower record data for those specimens for which this information was recorded. As can be seen, most of the flowers do not need a long tongue or face for their nectar to be accessible to the bees. However, a few individuals have been collected from long corolla flowers such as the labiate *Nepeta cilicica* and for none of the observations was it definitively recorded whether the bees were collecting pollen or nectar.

Distribution.—Localities where *T. prog-*

nathus was found and also those for which museum records are available are shown in Figure 1. The species appears to be common in northern Israel, particularly in the Upper Galilee and Golan Heights where it occurs at a wide variety of altitudes, from just a few hundred metres above sea level as at Katzrin to over 1,000m at the summit of Mt. Meiron. It has also been collected at 1650m on Mt. Hermon. There is a single male from Jerusalem, collected in the 1940's.

Phenology and dissection data.—Figures 2 and 3 plot head width and wing wear against date of capture for all females available for study. The data are consistent with overwintered females becoming active in March, becoming increasingly worn as they forage through to mid May and with the first individuals of the next generation flying from mid May until June for mating and pre-diapause feeding. Midseason females (worn individuals collected in May) are not smaller than those found earlier in the year (mean head width early bees = 2.31mm, SD = 0.05, n = 18; midseason bees = 2.33mm, SD = 0.06, n = 37; t = 1.80, p > 0.05). In fact, in this instance the direction of the size difference is in the opposite direction to that

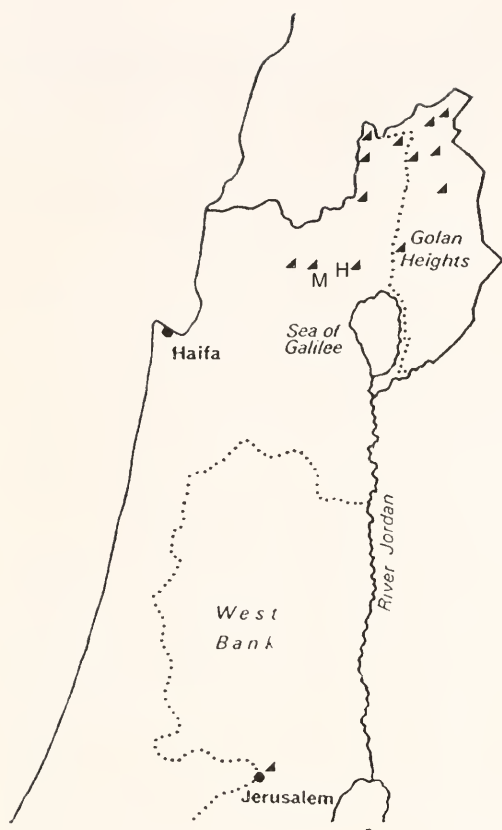


Fig. 1. Map of Israel showing location of sites where *T. prognathus* has been collected. H refers to Hazor and M to Mount Meiron, the two localities where most of the data dealt with in the text were obtained.

expected if midseason bees were workers and early season ones gynes. Similarly, worn late females are no smaller than the unworn pre-overwintering females (Mann-Whitney U test, $U = 87$, $t = 0.39$, $p > 0.5$); a size difference would be expected if the worn bees were workers and the unworn ones overwintering future foundresses. Thus, there is no size variation suggestive of the caste differences found in annual eusocial species.

A total of 20 bees from Hazor collected between May 7th and 10th (an additional 10 were pinned) and 17 from Mt. Meiron collected on June 2nd (an additional 8 were pinned) were dissected. All Hazor bees were well worn with an average wing

wear of 10.2 (SD = 4.5, $n = 30$). All formaldehyde preserved bees were mated and had well developed ovaries and 15 of them (75%) had a chorionated oocyte and at least one more ovariole with either a healthy oocyte developing or a sizeable resorbing oocyte. The remaining five bees each contained at least one oocyte three quarters the size of a fully developed one. The average size of the 20 dissected bees was 2.33mm (SD = 0.07) these results change almost imperceptibly when pinned specimens are added to the sample, mean size = 2.32 mm (SD = 0.06, $n = 30$). No *T. prognathus* were found at Hazor between May 28th and 30th, almost no flowers remained in bloom at this time. These data are consistent with the May Hazor samples being composed of foraging bees which had been active for at least several weeks and which were reproductive individuals. That no males were found suggests that the sample dates preceded the emergence of the next generation.

In contrast, the sample from Mt. Meiron at the beginning of June contained mostly unworn bees (22/25 or 88%) or bees with a total index of wear of one (2/25). Only one bee was well worn and it had 24 nicks in the wing margin. All bees in this sample were mated and all but the heavily worn individual had no ovarian development, large amounts of fat in their abdomens and a crop full of nectar. The exception had two $\frac{3}{4}$ developed oocytes that were resorbing, its abdomen contained no obvious large fat deposits and its crop was empty. The average size of the Mt. Meiron sample is identical to that of the one from Hazor (mean size = 2.33mm, SD = 0.06, $n = 25$). These data are consistent with the sampling period having occurred during the emergence phase of the offspring generation with only one individual of the parental generation captured.

None of the bees dissected showed any evidence of oophagy; they did not contain pasty-white material in their guts.

Table 2. Comparison of the frequencies of passing and agonistic interactions among paired individuals of various halictine species. Pass/FE is the frequency of successful passes per frontal encounter, A/FE is the frequency of aggressive interaction per frontal encounter.

Taxon	pss/FE	A/FE	Reference
Eusocial Species			
<i>L. zephyrum</i> queens	0.57	1.28	Breed et al. 1978
<i>L. zephyrum</i> foragers	0.21	0.56	Breed et al. 1978
<i>L. zephyrum</i> guards	0.00	0.61	Breed et al. 1978
Communal Species			
<i>L. hemichalceum</i>	0.81	0.02	Kukuk 1992
Solitary Species			
<i>L. figueresi</i>	0.14	0.41	Wcislo 1997b
<i>L. platycephalum</i>	0.30	0.11	McConnell-Garner
<i>L. (Ctenonomia) sp.</i>	0.33	0.22	and Kukuk 1997
Species With Unknown Behaviour			
<i>T. prognathus</i>	0.03	0.29	this paper

Bees collected and pinned from other samples also have the same size profile as those from samples discussed above, 34 bees from a variety of localities had an average head width of 2.32mm (SD = 0.06).

The first male was found at Ramot Naftali on May 12th, 7 more were found there on June 1st and one was collected at Mt. Meiron on June 2nd. All of these males were comparatively unworn. Few other records are available, but it seems that the first Ramot Naftali specimen is the earliest record and that males may be found until early July (Bluethgen 1955).

Behavioural observations.—A total of 218 encounters between paired bees in five circle tube experiments were observed. Thirty-four of these were C postures, 28 were nudges or lunges and 2 were pushes. Fewer cooperative behaviours were observed: 7 examples of back and follow and 6 successful passes, most of which were preceded by pass attempts; a total of 7 encounters resulted in pass attempts which failed and led to one or both of the bees backing off. Thus, 29.4% of all interactions were classified as antagonistic (varying between 10 and 35% among the pairs) and only 3% were passes (varying between 0 and 7%). The remainder involved one or

both bees turning away and may thus be considered as avoidance behaviours. The relative frequency of agonistic and cooperative behaviours did not vary much among the pairs, with the former always exceeding the latter.

Comparisons of successful passes and aggressive acts per encounter are shown in table 2 for those halictines for which such data are available. The behaviour of *T. prognathus* shows the lowest rate of passing (except for guard:guard pairs in *L. zephyrum*) and a level of aggressive interaction that falls within the range for solitary species and outside that for either communal or eusocial taxa.

DISCUSSION

Thrincohalictus prognathus has been considered to be a rare species likely to have a preference for flowers with a long corolla. However, observations in northern Israel confirm that it is widespread (Figure 1) and often common and that it does not have a preference for long tubular flowers (Table 1).

In solitary and communal halictine bees, all individuals in a sample collected from flowers may be expected to be of similar age (except during a period of overlap of

generations) and show similar evidence of reproductive activity. Early season samples should be of mostly unworn bees with average wear increasing monotonically until late in the season when the young offspring generation individuals fly to mate and to forage to fill their crops with nectar. At this time, bimodality in wear may be expected if some of the parental generation individuals have survived and are active. In samples of a eusocial species, early samples may be expected to show evidence of reproduction and comparatively little heavy wear, mid-season samples should show varying proportions of reproductively inactive individuals and a wide range of indices of wear and the latest samples should comprise mostly unworn pre-diapause females and some heavily worn ageing workers. Additionally, bees in samples of eusocial species taken in mid season should average smaller than those collected in spring as workers are usually smaller than nest foundresses (Breed 1975) (although the size difference varies from requiring large sample sizes to achieve statistical significance (Eickwort 1985) to being non-overlapping such that individuals can be classified as queens or workers on size alone (Knerer 1992)).

The samples of *T. prognathus* show no evidence of eusociality. The earliest specimen found was collected in mid March. Most samples are from early May and bees at this time are well worn but show substantial and largely equivalent levels of reproductive development. No unmated or ovarially undeveloped individuals have been detected at this time, which, being just prior to the apparent emergence of the overwintering brood, should have consisted entirely, or almost entirely, of workers if the species were eusocial. Although data on recently emerged brood are mostly from a separate and higher altitude (though nearby) locality, they indicate that foraging by females of this species has ceased by early June and that

males are actively searching for overwintering females at this time. In most of the region under discussion here, there are almost no flowers available for bee foraging after early June. Indeed, there was an extremely marked deterioration of forage availability at Hazor between early May and the end of the month such that great bee abundance had changed to an almost complete absence, several hours of searching between May 28th and 30th failed to result in any *T. prognathus* being found whereas earlier in the month several dozens could be observed in an hour.

Thus, based upon phenology, dissection and wear data, I conclude that *T. prognathus* is not an eusocial species in Israel. I now turn to the behavioural interactions among individuals observed in circle tubes.

Behavioural profiles of bees in circle tubes seem to reflect the differences between the conflictive relationships in eusocial and semisocial societies and harmonious interactions in communal ones (Kukuk and Crozier 1990; McConnell-Garner and Kukuk 1997; Paxton et al. 1999). In eusocial societies, where competition among individuals over oviposition or the sex ratio of brood occurs, agonistic acts such as C-postures, lunges and pushing are common (McConnell-Garner and Kukuk 1997; Pabalan et al. submitted). Conversely, communal species are much more tolerant, pass one another readily (Paxton et al. 1999) and unrelated individuals have even been observed performing trophallaxis (Kukuk and Crozier 1990). Solitary species show intermediate levels of both aggressive and cooperative behaviours (Table 2).

As noted above, the phenological and dissection data suggest that *T. prognathus* is not eusocial or semisocial. Similarly, communal behaviour would seem to be unlikely as the pass per encounter rates of bees with this type of colony organisation are consistently high (McConnell-Garner and Kukuk 1997; Packer unpublished ob-

servations) yet in *T. prognathus* they are the lowest recorded except for pairs of guards which are expected not to pass one another. Thus, I conclude that the data are most consistent with the hypothesis that this species is solitary. Clearly more detailed information is required and knowledge of the nest architecture of *T. prognathus* would also be of interest.

In conclusion, *T. prognathus* would seem to be a locally abundant halictine in northern Israel, it does not seem to specialise on pollen or nectar from long corolla plants and its phenology and behavioural patterns in experimental arenas are consistent with it being a solitary species, although forms of quasisocial behaviour cannot be definitively disproven.

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Sperm Development and Ultrastructure of Mature Spermatozoa of *Megalyra* (Hymenoptera: Megalyroidea)

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Abstract.—Sperm ultrastructure and aspects of spermiogenesis are described for the first time for a member of the hymenopteran superfamily Megalyroidea, the parasitic wasp, *Megalyra fasciipennis* Westwood. The Megalyroidea are a poorly-known, putatively ancient group of the Apocrita (wasp-waisted wasps), and they are the first member of the Evaniomorpha group of superfamilies (*sensu* Rasnitsyn 1988) whose sperm have been investigated in detail. Therefore their spermatology might provide clues as to the groundplan for the higher Hymenoptera.

The Megalyroidea are among the more elusive and least well known of the parasitic wasps, currently placed in the informal 'Evaniomorpha' group of superfamilies as defined by Rasnitsyn (1988) which comprises the Ceraphronoidea, Evanoidea s.l., Megalyroidea, Stephanoidea and Trigonalioidea. However, few characters are known that unite this morphologically and biologically heterogeneous group, and its monophyly is only weakly supported (Ronquist et al. 1999). How the Megalyroidea are related to the other apocritan (wasp-waisted) Hymenoptera is therefore not well understood, and several features suggest that they may be one of the most basal groups, forming a transition between the parasitic sawfly family Orussidae and the other parasitic wasps (see Gibson 1985; Shaw 1990; Heraty et al. 1994; Downton & Austin 1994; Vilhelmsen 1997). Few species are known and most are known from only one or a few specimens in collections (Shaw 1990). They are idiobiont ectoparasitoids of concealed hosts, probably the majority attacking the wood-boring larvae of large beetles including the pest cerambycid, *Phoracantha*

(Shaw 1990; Austin *et al.* 1994). Introductions of one Australian species, *Megalyra fasciipennis* Westwood, into South Africa in an attempt at biological control of *Phoracantha* has resulted in a population of the parasitoid that in some years becomes numerous enough to permit guaranteed and relatively straightforward collecting, and it was in one of those years that material was obtained for spermatological investigation. This study provides the first spermatological information on the Megalyroidea, and is also the first detailed ultrastructural investigation of sperm for any of the 'Evaniomorpha' superfamilies. The work was carried out to provide basic ultrastructural information on sperm development in this rarely studied group, and to see if comparison with other Apocrita can provide phylogenetic information.

That sperm ultrastructure might provide new character systems for resolving relationships within the Hymenoptera was muted by Jamieson (1987), it was not until the preliminary comparative survey of non-aculeates by Quicke et al. (1992) that some of the wealth of characters they possess became apparent. But, while a grow-

ing number of superfamilies of Hymenoptera have had at least one included species examined in detail for sperm ultrastructure (see for example, Thompson & Blum 1967; Lensky et al. 1979; Lingmei & Dunsu 1987; Wheeler et al. 1990; Newman & Quicke 1998, 1999a,b) there are a number of important and phylogenetically significant groups for which nothing is known, for example, Orussoidea, Stephanoidea, Trigonaloida and even the Evanoidea, Ceraphronoidea, Cynipoidea and Platygastroidea, the last four of which are common and easy to obtain alive. It is hoped therefore that the present work will help encourage others to investigate the spermatology of these taxa in order to add to the body of phylogenetic information for resolving higher relationships within the order.

MATERIAL AND METHODS

Recently eclosed adult male *Megalyra fasciipennis* Westwood were collected in South Africa in September 1998 and transported by air to the U.K., where testes and vas deferens were dissected under 2% glutaraldehyde in phosphate buffered saline (pH 7.2), fixed for two hours, then transferred to 2% osmium tetroxide in cacodylate buffer (pH 7.2) for a further 2 hr fixation. After two buffer washes, tissue was dehydrated to 50% ethanol and then contrasted with a saturated solution of uranyl acetate in 50% ethanol prior to complete dehydration, embedding in Epon resin and polymerisation overnight. Large silver sections were picked up on high resolution grids and contrasted with uranyl acetate and lead citrate.

RESULTS

Mature sperm of *Megalyra fasciipennis* collected from the vas deferens were not formed into spermatodesmata. The individual sperm ranged in length from 160 to 200 μm , though most were close to 180 μm of which the head (acrosome plus nucleus) constituted approximately 17%. The head

was not much wider than the tail at its widest and could be seen to taper from the posterior of the nucleus to the tip of the acrosome.

The mature sperm of *Megalyra* (Fig. 1), illustrate all of the organelles so far described in the sperm of other parasitic wasps, i.e. axoneme, mitochondrial derivatives, deltoid bodies, acrosome and nucleus. In the testes cysts are found with sperm at many different stages of development. Primary and secondary spermatocytes are found with the latter in a syncytium formed by incomplete cytogenesis following the earlier mitotic division (Fig. 2). The structural features are as follows:

Axoneme.—The tail portion of the mature sperm contains a single axoneme with a $9 + 9 + 2$ arrangement of microtubules for most of its length (Fig. 3). There are well developed accessory structures, particularly linking the central pair of microtubules (Fig. 3, *arrowed*).

The axoneme develops from an electron dense structure which becomes positioned adjacent to the nucleus defining the posterior pole of the nucleus (Fig. 4). This structure, often referred to as a ring centriole (Fig. 5), contains the basal body of the axoneme, from which the axoneme elongates. However, during spermiogenesis, many sectioned cells are found with between two and four axoneme profiles (Fig. 6). Usually one or more of the profiles exhibits a loss of structural integrity (*arrowed* Fig. 6) often appearing with less than the full complement of microtubules. It is not exactly clear what these represent and the possibility that they are degenerating cells cannot be ruled out, though their prevalence and the presence in each of at least one apparently perfect axoneme profile suggest that they are a normal developmental stage. No mature sperm with multiple tails have been found.

Mitochondrial derivatives and centriolar adjunct.—The mature sperm has two differently sized crystalloid mitochondrial de-

rivatives (Figs. 1 & 3), which run for the length of the tail. The larger of the two mitochondrial derivatives also runs into the head of the sperm, parallel to the nucleus (Fig. 7). In transverse section (Fig. 8) it can be seen that the mitochondrial derivative can occupy a greater proportion of the shaft area than the nucleus itself (Fig. 8, *arrowed*).

The mitochondrial derivatives are derived from a Nebenkern, the product of the fusion of large numbers of small mitochondria in the early spermatid. Unlike other sperm so far reported, the Nebenkern goes through a stage where the mitochondrial material forms a tube, before producing the asymmetrically-sized mitochondrial derivatives (Fig. 9, *arrowed*). The association between the larger mitochondrial derivative and the nucleus is evident from the earliest stages of nuclear shape change (Fig. 10). Mitochondrial material

appears to be present at the locus of this change.

The centriolar adjunct in the adult sperm is positioned between the smaller mitochondrial derivative and the nucleus (Fig. 1). During development there is a close association between the centriolar adjunct and the developing axoneme (Fig. 11). In the cells where with multiple axonemes additional centriolar adjuncts are also present (Fig. 12) indicative of the close association between the two organelles.

Nucleus.—Axoneme development commences before nuclear elongation which follows a similar pattern to that described for the braconid *Aleiodes*, with the formation of lateral plates (Fig. 10) opposite aggregations of dense chromatin strands (*cf* Newman & Quicke 1998).

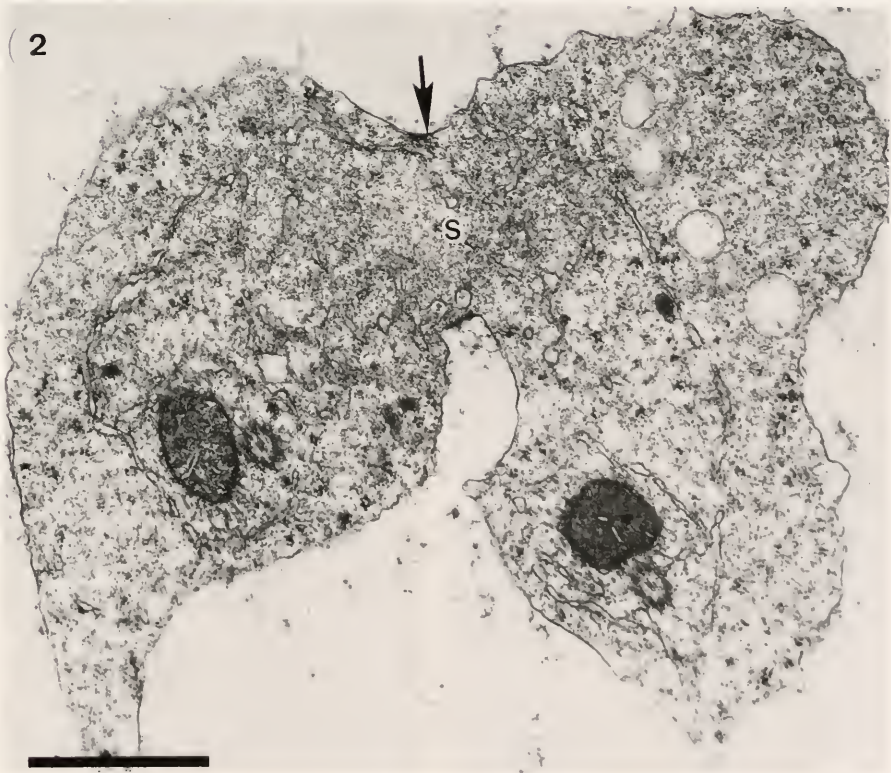
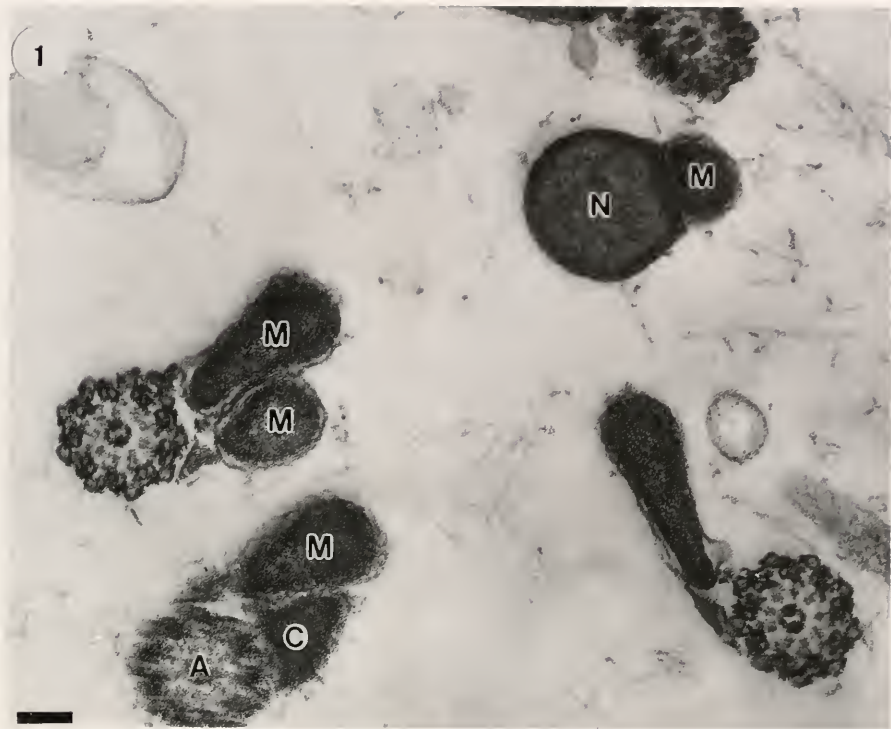
Acrosome.—The acrosome forms from fusion of small vesicles at the posterior

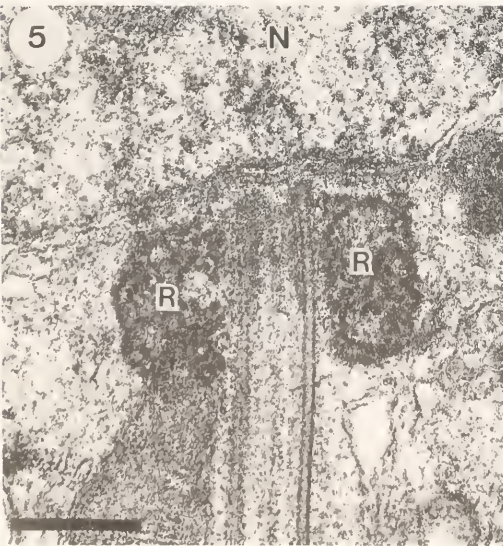
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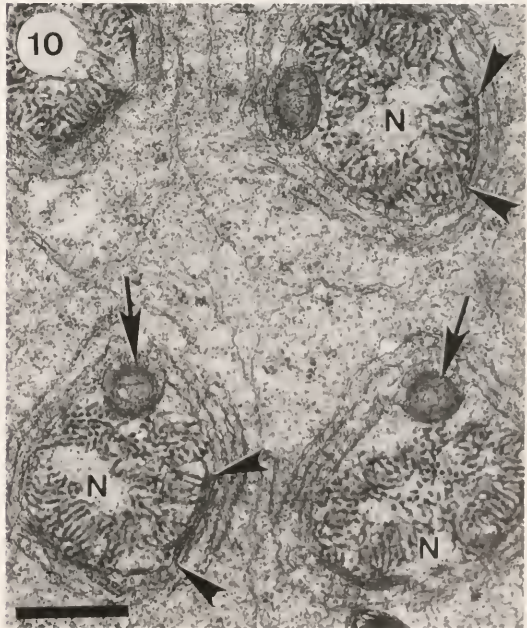
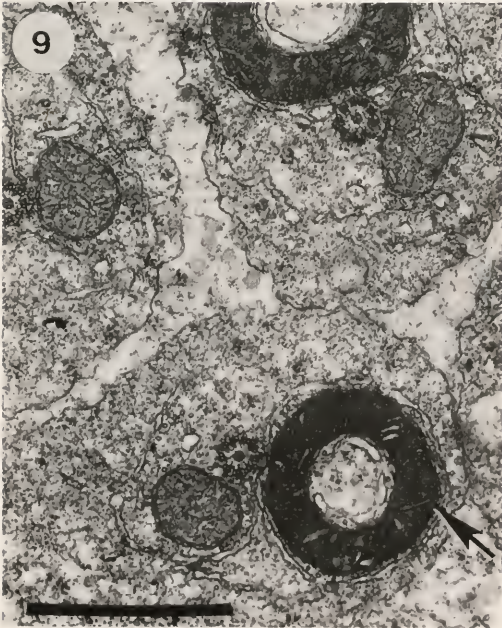
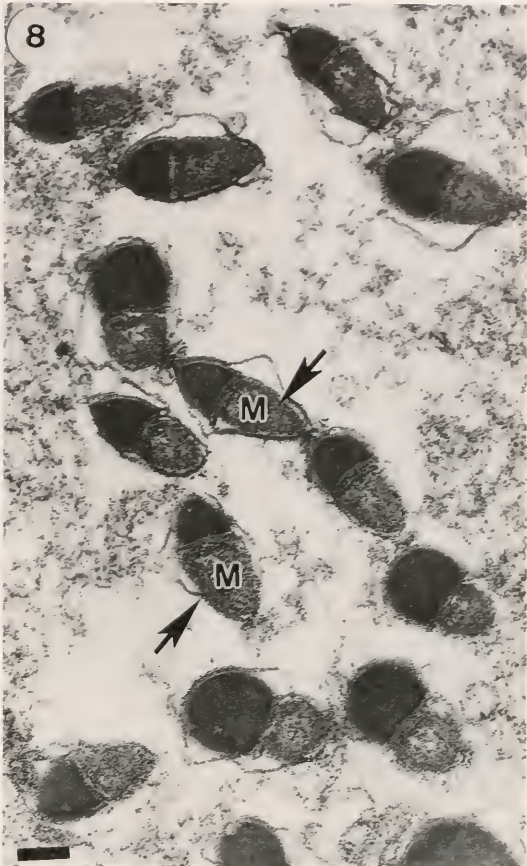
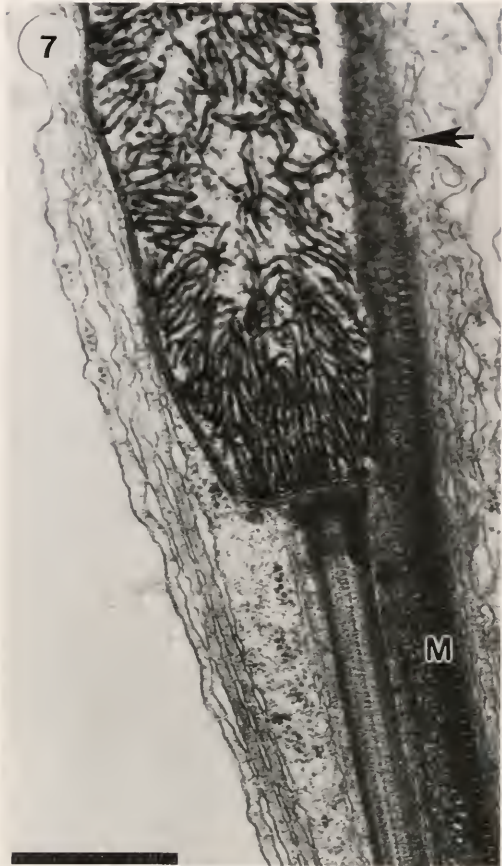
Figs. 1–2. Mature sperm and early spermiogenesis of *Megalyra*: 1, transversely sectioned vas deferens with mature sperm with axonemes (A), nucleus (N), asymmetrically sized mitochondrial derivatives (M)—including some with only one mitochondrial derivative (*arrowed*)—and centriolar adjunct (C) in some sections where it occupies the position of the smaller mitochondrial derivative just posterior to the nucleus (scale bar = 100 nm); 2, secondary spermatocytes forming a syncytium (S) because of incomplete cytokinesis following the earlier mitotic division, the thickened membrane (*arrowed*) indicating intercellular bridges (scale bar = 0.5 μ m).

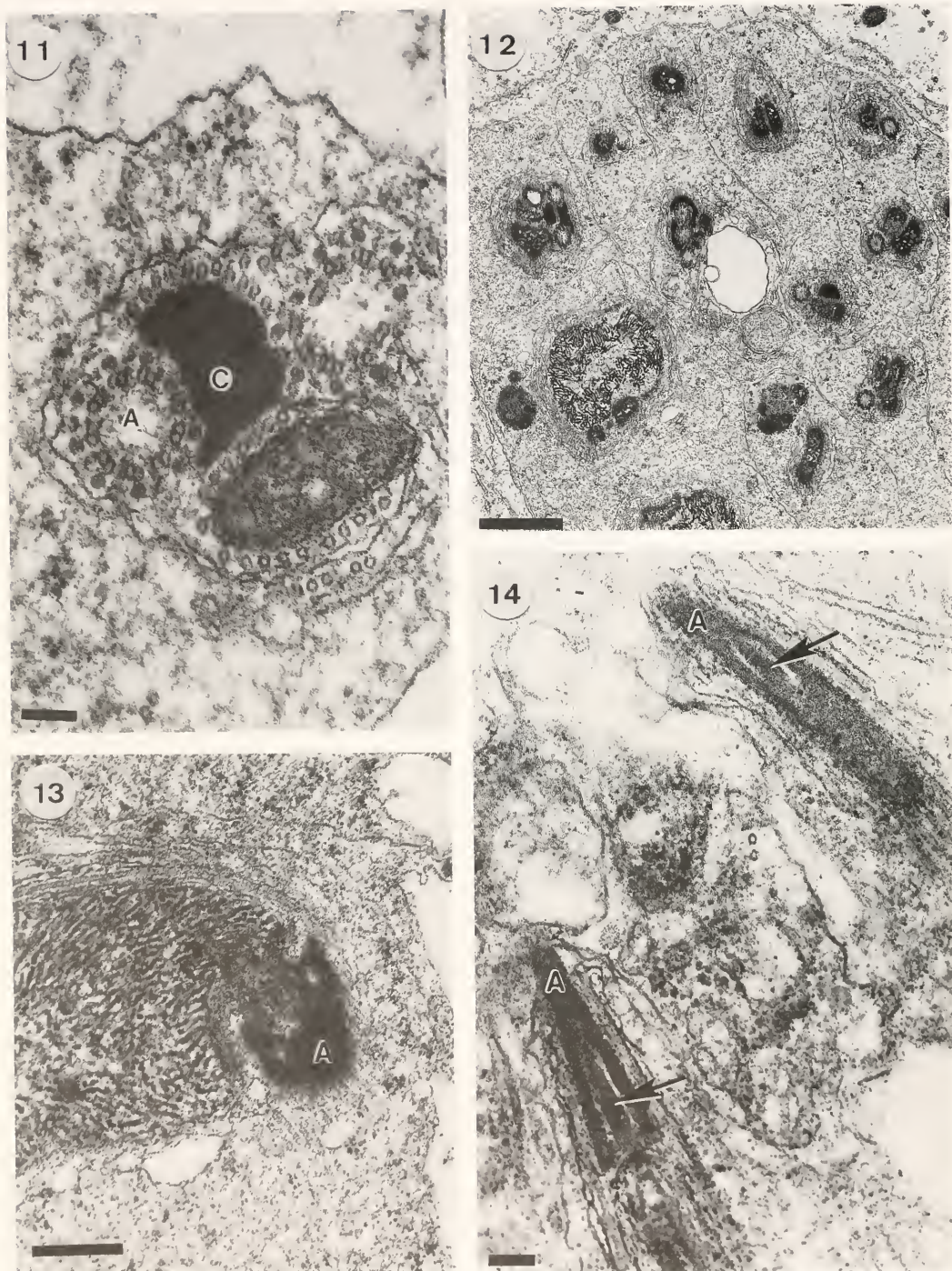
Figs. 3–6. Various stages in spermiogenesis of *Megalyra*: 3, transverse section of the tail portion of mature sperm illustrating the 9 + 9 + 2 arrangement of microtubules, with accessory filaments evident, particularly linking the central pair of microtubules (*arrow*), and with two deltoid bodies (D) in association with the mitochondrial derivatives (scale bar = 100 nm); 4, early spermatid illustrating the growth of the axoneme (*arrowed*) from a position at the posterior pole of the nucleus (N) (scale bar = 500 nm); 5, early spermatid showing ring centriole (R) surrounding the basal body of the developing axoneme (scale bar = 250 nm); 6, during development many cell sections show multiple axoneme profiles (A), closer than would be expected if they represented sections through a single convoluted structure—note disruption of one of the profiles (*arrowed*) (scale bar = 100 nm).

Figs. 7–10. Various stages in spermiogenesis of *Megalyra*: 7, longitudinal section of the sperm head piece with the larger mitochondrial derivative (M) extending from the tail portion, where it is found adjacent to the axoneme, and then running parallel to the nucleus (*arrowed*) (scale bar = 0.5 μ m); 8, transverse section through mature spermatozoan illustrating differences in the size of the nucleus (N) and of the large mitochondrial derivative (M) in the head portion of the sperm in the region of overlap between the two (scale bar = 100 nm); 9, transverse section of early spermatid illustrating a stage during formation of the mitochondrial derivatives when the Nebenkern becomes tubular (*arrowed*) (scale bar = 1 μ m); 10, one mitochondrial derivative (*arrowed*) lies partly in a groove along the nucleus during earlier stages of development—note also the lateral plates (between arrowheads) which appear to be anchor sites for condensed chromatin during nuclear shape change (scale bar = 0.5 μ m).









Figs. 11-14. Various stages in spermiogenesis of *Megalyra*: 11, transverse section of spermatid illustrating how the centriolar adjunct (C) is closely associated with the axoneme (A) during development (scale bar = 100 nm); 12, developing cyst of spermatids showing that cells with multiple axonemes have accompanying centriolar adjuncts (scale bar = 1 μ m); 13, during development the acrosome (A) is formed from the fusion of small vesicles and becomes positioned at the anterior pole of the nucleus (scale bar = 0.5 μ m); 14, acrosome in longitudinal section (A) covering the perforatorium (arrowed) (scale bar = 100 nm).

pole of the nucleus (Fig. 13). Although it develops a perforatorium (Fig. 14, *arrow*), the acrosome is small and ill-developed in comparison with the rest of the sperm and was very hard to find despite searching hundreds of transverse sections.

DISCUSSION

The presence of two markedly differently sized mitochondrial derivatives has been reported in other parasitic wasps' spermatozoa, e.g. *Leptopilina*, which belongs to the only distantly related superfamily Cynipoidea (Newman and Quicke 1999b). We have also found a similar arrangement in the sperm of the xyelid sawfly, *Xyela julii* (Newman and Quicke 1999a). Whether this feature could be considered 'primitive' is doubtful given that other sawflies (*Cephalcia* of the Pamphiliidae and *Tremex* of the Siricidae) have equally sized mitochondrial derivatives.

The large length of overlap between one of the mitochondrial derivatives and the nucleus has only been found in sperm of one other parasitic wasp, the distantly related chalcidoid wasp genus *Trichogramma* (Lingmei & Dunsu 1987). The cynipoid, *Leptopilina*, which also has asymmetric sized mitochondrial derivatives, also has an overlap of nucleus and mitochondrial derivative, but over a much smaller distance (Newman & Quicke 1999b).

This intimate relationship of mitochondrial material and nucleus exists from an early stage of spermiogenesis. The mitochondrial material is found at the focus of the nuclear shape change which occurs during cell elongation, where the nucleus curves into a horse-shoe shape, a shape change similar to that found in *Aleiodes* (Newman & Quicke 1998). One aspect of development which has not been previously reported is the occurrence of tubular elements in the Nebenkern after fusion of the small mitochondria of the early spermatid. This is probably an apomorphic character state and it may be of potential

phylogenetic significance within the Euanimorpha.

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Afrotropical Ants (Hymenoptera: Formicidae): Taxonomic Progress and Estimation of Species Richness

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Abstract.—Forty-three of the 82 Afrotropical ant genera (52%) have been revised to modern standards resulting in a 50% increase in number of species. There are currently 1705 species of ants known from the Afrotropical region, a figure that could increase to over 2136 species if all ant genera receive a modern revision. To incorporate all undescribed species, total Afrotropical ant species richness was calculated by extrapolating from data on the proportion of undescribed species collected at Mkomazi Game Reserve in Tanzania and the Cape of Good Hope section of the Cape Peninsula National Park in South Africa. On this basis there are an estimated 3105 species of ants in the Afrotropical region, with 45% undescribed or currently occupying an infraspecific taxonomic rank. This extrapolation assumes that the average range sizes of described and undescribed species are similar, which in reality is unlikely because widely distributed species are more likely to have been collected and described. I present a method that distinguishes between widespread and localised species to correct for this problem, which extrapolates 4093 Afrotropical ants species, with 58% of species estimated to be undescribed or currently recognised only at infraspecific rank. It would take a highly productive systematist at least 21 years to complete revisions of the unrevised ant genera. A strategy is presented for improving specimen collection and taxonomy of Afrotropical ants.

Until recently, working on the taxonomy of ants and identifying them to genus was hindered by poor, out-dated catalogues and inadequate keys. Ant systematists, however, now have three books that provide a synthesis of our current knowledge: Bolton has produced keys to ant genera of the world (Bolton 1994) and a catalogue of world ants (Bolton 1995b) and Ward *et al.* (1996) have provided a thoroughly researched bibliography of ant taxonomic literature. In addition, the book by Shattuck (1999) makes identification of Australian ant genera much easier than before.

Despite the relative ease with which ants can now be identified to genus, species identification is much more difficult because many ant genera have not been recently revised. Species-level identifications in recently revised genera can also

be problematic when such revisions are based on collections with limited geographic coverage that omit species and population variation. Older taxonomic works (mainly pre-1965) are difficult to use for identifying species because they are often burdened with poorly applied quadrinomials (genus, species, subspecies, variety) that do not correspond with evolutionary relationships. With the catalogue by Bolton (1995b), the bibliography by Ward *et al.* (1996), and a wealth of new material collected using modern survey methods, the tools are available to tackle the revision of neglected ant genera. However, at present there is no strategy in place for accomplishing this remaining work and basic information on approximately how much work remains is necessary for establishing goals and priorities. Although Bolton (1995a) has provided a

taxonomic and zoogeographical census of documented ant diversity, he did not assess the current taxonomic health of all ants, nor does he address the issues of the proportion of ant genera that lack modern taxonomic treatment, and the effort that such treatment will require.

In addition to our inability to estimate the effort that will be required to revise all ant genera to modern taxonomic standards, we are also unable to reliably estimate how many ant species exist and how many are undescribed. On a world level, Gauld & Bolton (1988) estimated 15,000, and Hölldobler and Wilson (1990) estimated 20,000 species in total, these estimates being largely intuitive. By the end of 1993, 9538 described valid ant species in the world were recognised (Bolton 1995a), so according to the above two estimates, 36–52% of ant species either remain undescribed or currently occupy an infraspecific rank.

Estimates of total diversity are often made using data from particular localities where it has been possible to estimate the proportion of species that are undescribed, and to use this proportion to extrapolate to a wider level (e.g. Hodkinson and Casson 1991, Hodkinson 1992 for Hemiptera). This approach implies that the average range sizes of described and undescribed species are similar (Hodkinson and Hodkinson 1993; Hammond 1995). In practice, this is highly unlikely as widely distributed species are more likely to be captured and described than species with more localised distributions. Hodkinson and Hodkinson (1993) examined this problem by comparing data from two sites and providing a statistical test of whether the probability of capture of described species was different from the probability of capture of undescribed species and then using the ratio of these two probabilities to adjust the final estimate of species diversity. The outcome of such a comparison depends largely on the similarity and proximity of the two sites. An

alternative approach, which involves distinguishing between widespread and localised species, is presented here to address the problem of range size differences between described and undescribed species.

The Afrotropical region is defined here according to Bolton (1994) as Africa south of the Sahara and the southern half of the Saudi Arabian Peninsula. Madagascar and its nearby islands are excluded. Our knowledge of the ant fauna of this region is the product mainly of the following taxonomists (see Ward *et al.* 1996 for publication details): F. Smith (1851–1879); Mayr (1853–1908); Forel (1869–1920's); Emery (1869–1926); Santschi (1906–1941); Arnold (1905–1962, including "A monograph of the Formicidae of South Africa", published 1915–1926); Brown (1943–1995); and Bolton (published 1969 to present).

The present paper is aimed at establishing the current level of taxonomic knowledge of Afrotropical ant species by assessing the proportion of ant genera that remain to be revised to modern taxonomic standards and the effort required to undertake these revisions. In addition, I estimate total ant species richness in the Afrotropical region using data on the proportion of undescribed species collected at two widely separated localities in Africa, namely Mkomazi Game Reserve in Tanzania and the Cape of Good Hope section of the Cape Peninsula National Park in South Africa. At both sites, ants have been intensively collected using a variety of methods, thereby increasing the probability that the observed ratio of undescribed to described species is a good estimate of the ratio for those species that have not been collected. I conclude by suggesting a strategy for improving both the collecting and the taxonomic treatment of Afrotropical ants.

METHODS

Estimation of species number increment from revision of genera.—I divided the Af-

rotropical ant genera between those that have received a modern revision (defined here as from 1965 onwards) and those that have not; revisions prior to 1965 are either incomplete or use the old quadrinomial system. Genera represented only by introduced species (*Linepithema humile* (Mayr), *Wasmannia auropunctata* (Roger)) have been excluded. Genera that have received a modern revision are henceforth referred to as 'revised genera' and the remaining genera as 'unrevised genera'. For each revised genus I calculated the species increment coefficient, i.e. the number of valid species divided by the number prior to revision. Descriptions of new species and the raising of subspecies to species increased the increment coefficient whereas synonymising of previously valid species decreased it. Lowering of rank from species to subspecies was not encountered in any of the revisions. In genera which have received more than one revision since 1970 (e.g. *Ocymyrmex*), I calculated the number of valid species before the first revision and the number by completion of the last revision. Subsequent papers describing additional new species in revised genera were also included in the analysis. An increment coefficient for all revised genera was calculated based on the total number of valid species before and after for all revisions and new descriptions.

For unrevised genera, I counted the number of valid species and multiplied this by the increment coefficient for revised genera to arrive at an estimate of the total number of species after revision. The total species for the revised genera plus this estimated value for the unrevised genera gives the 'Total estimated revised species'.

Estimation of total species richness.—An estimate of total ant species richness in the Afrotropical region was obtained by determination of the proportions of described and undescribed species in Mkomazi Game Reserve, Tanzania, and in the

Cape of Good Hope section of the Cape Peninsula National Park, South Africa.

Ants were collected in Mkomazi Game Reserve using pitfall traps, malaise traps, Winkler bag leaf litter extractions, soil sieving, light traps, sweeping, and collecting by hand (Robertson 1999). Mkomazi Game Reserve has a wide range of vegetation types such as grassland, open and closed woodland, and hilltop forest. It lies in a region that does not have a long history of ant collecting although the vegetation types it contains have been sampled in other regions such as Kenya and Zimbabwe.

The Cape of Good Hope section of the Cape Peninsula National Park consists of mesic mountain fynbos, west coast strandveld and a few relict small patches of indigenous evergreen forest. Because of its position near the southern tip of Africa, many naturalists have collected in the Cape Peninsula and one might thus expect the ant fauna to be well known. However, many cryptic species went unnoticed until the recent systematic use of collecting methods such as pitfall trapping and Winkler bag leaf litter extraction.

For each of these two localities, I determined the ratio of undescribed species that belong to revised genera:

$$U/K = u/k$$

Therefore

$$U = u(K/k)$$

where U is the number of undescribed species in the Afrotropical region, u is the number of undescribed species at the locality, K is the number of known (i.e. valid) species in the Afrotropical region and k is the number of known species at the locality. As already discussed, this approach assumes that the average range size of known and undescribed species is similar (Hodkinson and Hodkinson 1993; Hammond 1995) which in reality is unlikely because widely distributed species would be more likely to have been col-

lected and described. In order to reduce the bias, I arbitrarily categorised all known Afrotropical species in revised genera between 'widespread species' that have recorded distributions over three or more countries and 'localised species' that have been recorded from only one or two countries (based on information obtained from the revisions as well as from records in the South African Museum ant computer database). The average range size of the localised species is likely to be more similar to the average range size of the undescribed species than that of all known species together. By reducing the bias in this way, the ratio of undescribed to localised species at an Afrotropical level should therefore be similar to the ratio of undescribed to localised species at a local level and therefore

$$U = u(L/l)$$

where, for recently revised genera, L is the number of localised known species in the Afrotropical region and l is the number of localised known species at a particular locality.

Accumulation of described species as a function of collecting date.—As an alternative way of assessing the proportion of ant species that are still undescribed, for a sample of revised genera I recorded the year the type was collected for each valid species and plotted the accumulation of species as a function of collection date. The collection date was not recorded for many of the earlier types and for these I used the publication date instead. The early ant taxonomists such as Emery and For-el usually provided descriptions for new species within one or two years subsequent to their collection.

Time taken to revise genera.—In order to estimate the time that it would take to revise the unrevised ant genera, I analysed the productivity of the world's most productive ant systematist, Barry Bolton, who has also done most of the revisionary work on Afrotropical ants. During the 16

years from 1972 to 1987 he worked single-mindedly at revising various ant genera. For each of his taxonomic publications during this period, irrespective of whether they concerned Afrotropical ants, I recorded the number of valid species before the revision, the number of new species described and the number of valid species resulting from the revision. The number of valid species in an unrevised genus divided by the average number of initial valid species processed per year by Bolton, gives the number of years it would take to revise the genus (at maximum productivity).

RESULTS

Estimation of species number increment from revision of genera.—Modern revision of 43 (52%) of the Afrotropical ant genera has resulted in an overall 50% increase in number of species, so that the number of species at the completion of the revisions was 1.5 times greater than the initial number (Table 1). At the one extreme are genera such as *Anochetus*, *Psolidomyrmex*, *Pristomyrmex* and *Platythyrea* that decreased in number of species as a result of species being synonymised in the revision. At the other extreme are genera such as *Axinidris*, *Cyphoidris*, *Ocymyrmex*, *Paedalgus*, *Pyramica* and *Strumigenys* that more than doubled in size mainly as a result of the description of new species.

There are 862 valid species in the 39 (48%) unrevised Afrotropical genera (Table 2) and as the initial number of species in the revised genera amounted to 561 (Table 1), based on the relative number of species we are therefore about 39% of the way through revision of the genera to modern standards. Revision of the unrevised genera over a similar time period as the revised genera would have swelled the number of species from 862 species to about 1293 (Table 2). Together with the 843 species in the revised genera (Table 1) there is a total of 2136 estimated revised species, an increase of 20% over the 1705

Table 1. List of the Afrotropical ant genera that have received one or more modern taxonomic revisions (1965 onwards). The initial number of valid species before the first modern revision, the final number of valid species known at present, and the increment coefficient (used in Table 2) are shown.

	Initial species	Final species	Increment coefficient (Final/Initial)	Modern revisions and subsequent publications of new species
<i>Afroxyidris</i>	0	1		Belshaw and Bolton (1994)
<i>Agraulomyrmex</i>	0	2		Prins (1983)
<i>Ankylomyrma</i>	0	1		Bolton (1973b, 1981b)
<i>Anochetus</i>	24	18	0.75	Brown (1978)
<i>Aphomomyrmex</i>	2	1	0.50	Snelling (1979b)
<i>Apomyrma</i>	0	1		Brown, Gotwald and Levieux (1971)
<i>Atopomyrmex</i>	2	3	1.50	Bolton (1981b); Snelling (1992)
<i>Axinidris</i>	3	13	4.33	Shattuck (1991)
<i>Baracidris</i>	0	2		Bolton (1981b)
<i>Bondroitia</i>	3	2	0.67	Bolton (1987)
<i>Calyptomyrmex</i>	13	16	1.23	Bolton (1981a)
<i>Camponotus (fulvopilosus-group)</i>	2	4	2.00	Robertson (1990); Robertson and Zachariades (1997)
<i>Cardiocondylia</i>	11	9	0.82	Bolton (1982)
<i>Cataulacus</i>	38	39	1.03	Bolton (1974a, 1982); Snelling (1979a)
<i>Concoctio</i>	0	1		Brown (1974a,b)
<i>Cyphoidris</i>	1	4	4.00	Bolton (1981b)
<i>Decamorium</i>	2	2	1.00	Bolton (1976)
<i>Dicroaspis</i>	2	2	1.00	Bolton (1981a)
<i>Diplomorium</i>	1	1	1.00	Bolton (1987)
<i>Doloponera</i>	0	1		Brown (1974c,d)
<i>Leptogenys</i>	32	56	1.75	Bolton (1975a)
<i>Leptothorax</i>	11	11	1.00	Bolton (1982)
<i>Melissotarsus</i>	6	3	0.50	Bolton (1982)
<i>Meranoplus</i>	9	8	0.89	Bolton (1981a)
<i>Messor</i>	14	14	1.00	Bolton (1982); Collingwood (1993)
<i>Microdaceton</i>	3	2	0.67	Bolton (1983)
<i>Monomorium</i>	90	149	1.66	Bolton (1987)
<i>Ocymyrmex</i>	12	37	3.08	Bolton (1981b); Bolton and Marsh (1989)
<i>Odontomachus</i>	1	2	2.00	Brown (1976)
<i>Paedalgus</i>	3	9	3.00	Bolton and Belshaw (1993)
<i>Petalomyrmex</i>	0	1		Snelling (1979b)
<i>Platythyrea</i>	15	14	0.93	Brown (1975)
<i>Plectroctena</i>	13	17	1.31	Bolton (1974b); Bolton, Gotwald and Leroux (1979)
<i>Polyrhachis</i>	43	47	1.09	Bolton (1973a)
<i>Pristomyrmex</i>	6	5	0.83	Bolton (1981b)
<i>Probolomyrmex</i>	3	3	1.00	Taylor (1965); Brown (1975)
<i>Pyramica</i>	24	63	2.63	Bolton (1983), Bolton (1999)
<i>Psalidomyrmex</i>	8	6	0.75	Bolton (1975b)
<i>Rhoptryrmex</i>	3	5	1.67	Bolton (1976, 1986)
<i>Simopone</i>	7	9	1.29	Brown (1975); Kutter (1976, 1977)
<i>Sphinctomyrmex</i>	1	2	2.00	Brown (1975)
<i>Strumigenys</i>	17	42	2.47	Bolton (1983), Bolton (1999)
<i>Terataner</i>	5	6	1.20	Bolton (1981b)
<i>Tetramorium</i>	131	209	1.60	Bolton (1976, 1980, 1985)
Total	561	843	1.50	

Table 2. Afrotropical ant genera that have not received a modern taxonomic revision. The number of estimated species after revision was calculated by multiplying the number of valid species currently known by the Increment coefficient (1.5) in Table 1. The minimum years to revise a genus is calculated on the basis that B. Bolton processed species (i.e. the number of species before a revision) at a rate of 42/year.

Genus	Number of valid species	Estimated species after revision	Years (minimum) to revise genus
<i>Acropyga</i>	2	3	0.05
<i>Aenictogiton</i>	7	11	0.17
<i>Aenictus</i>	34	51	0.81
<i>Amblyopone</i>	3	5	0.07
<i>Anoplolepis</i>	19	29	0.45
<i>Asphinctopone</i>	3	5	0.07
<i>Camponotus</i> (excl. <i>fulvopilosus</i> -group)	156	234	3.71
<i>Carebara</i>	11	17	0.26
<i>Cataglyphis</i>	1	2	0.02
<i>Centromyrmex</i>	5	8	0.12
<i>Cerapachys</i>	24	36	0.57
<i>Crematogaster</i>	129	194	3.07
<i>Cryptopone</i>	1	2	0.02
<i>Discothyrea</i>	7	11	0.17
<i>Dorylus</i>	57	86	1.36
<i>Ecphorella</i>	1	2	0.02
<i>Hypoponera</i>	36	54	0.86
<i>Lepisiota</i>	45	68	1.07
<i>Leptanilla</i>	3	5	0.07
<i>Myrmicaria</i>	22	33	0.52
<i>Mystrium</i>	1	2	0.02
<i>Oecophylla</i>	1	2	0.02
<i>Oligomyrmex</i>	33	50	0.79
<i>Pachycondyla</i>	53	80	1.26
<i>Paratrechina</i>	13	20	0.31
<i>Phasmomyrmex</i>	4	6	0.10
<i>Pheidole</i>	66	99	1.57
<i>Pheidologeton</i>	7	11	0.17
<i>Phrynoponera</i>	5	8	0.12
<i>Plagiolepis</i>	18	27	0.43
<i>Prionopelta</i>	3	5	0.07
<i>Proceratium</i>	5	8	0.12
<i>Pseudolasius</i>	5	8	0.12
<i>Santschiella</i>	1	2	0.02
<i>Solenopsis</i>	10	15	0.24
<i>Streblognathus</i>	1	2	0.02
<i>Tapinoma</i>	13	20	0.31
<i>Technomyrmex</i>	25	38	0.60
<i>Tetraponera</i>	32	48	0.76
Total	862	1293	20.52

valid species currently known from the Afrotropical region.

Estimation of total species richness.—The percentage of undescribed species within recently revised genera is 30.9% for ants in Mkomazi Game Reserve and 32.3% for ants in Cape of Good Hope Nature Re-

serve (Table 3), remarkably similar values considering the distance between the two localities, the differences in their habitat complements and differing histories of ant collecting in the two regions. If these percentages are extrapolated to the unrevised genera, and the 50% increase from revis-

Table 3. Ant species diversity and composition in Mkomazi Game Reserve in Tanzania, Cape of Good Hope section of the Cape Peninsula National Park (CGH) in South Africa, and in the Afrotropical region as a whole.

	Mkomazi	CGH	Total	Afrotropical
All general:				
Total recorded species	232	72	303*	1705
Revised genera:				
No. widespread species	54	2	56	249
No. localized species	11	19	30	594
Total known species	65	21	86	843
% localized species	16.9	90.5	34.9	70.5
No. undescribed species	29	10	39	?
Total species	94	31	125	?
% undescribed species	30.9	32.3	31.2	?

* Only one species (*Technomyrmex albipes* (F. Smith)) shared between the two localities.

ing genera is taken into account, then the percentage of undescribed species for all genera is 44% for Mkomazi Game Reserve and 45% for Cape of Good Hope. Further collecting and analysis of ants at these localities is still taking place so the percentages above could change. There are considerable differences between the two localities in the proportion of known species in revised genera that have localised distributions covering only one or two countries (Table 3). Whereas only 16.9% of known species in Mkomazi Game Reserve have localised distributions, 90.5% of species in Cape of Good Hope Nature Reserve are localised. Many of the Mkomazi species are widely distributed in African savannahs, often ranging from the northern regions of South Africa through to Ethiopia or with a Sahel distribution from West Africa to Ethiopia and down into East Africa (Robertson 1999). The forest dwelling species also often have distributions extending into central Africa and other countries in East Africa. Conversely, many of the species in the Cape of Good Hope section of the Cape Peninsula National Park are limited to the Cape fynbos, or have distributions that extend only as far as Namaqualand or KwaZulu-Natal. In the Afrotropical region as a whole, 70.5% of species are localised (Table 3).

Based on the combined data from both Mkomazi Game Reserve and Cape of Good Hope, simple extrapolation of the proportion of undescribed species (using the formula $U = uK/k$) produces an estimated total of 3105 species for the Afrotropical region, whereas exclusion of the widespread species in the calculation of new species (using the formula $U = uL/l$) increases the total by 32% to produce an estimated total of 4093 species (Table 4). The estimated diversity using the latter formula on only the Mkomazi data is 6104 species, twice as high as the estimate based on only Cape of Good Hope, caused by the large difference between them in the ratio of widespread to localised species.

Based on the combined data from both localities, approximately 45–58% of ant species in the Afrotropical region are undescribed or are currently ranked as subspecies when they should be ranked as species (Table 4).

Accumulation of described species as a function of collecting date.—Analysis of the accumulation of described, valid species as a function of collecting date (Fig. 1) shows that undescribed species are being discovered at an undiminishing rate, with the species accumulation curve showing no signs of plateauing. The curve shows that

Table 4. Estimates of total ant species diversity in the Afrotropical region, based on the proportion of undescribed species in Mkomazi Game Reserve in Tanzania and in Cape of Good Hope section of the Cape Peninsula National Park (CGH) in South Africa (Table 3). The first estimate uses the ratio of total known species at a regional and local level and the second the ratio of localized known species (defined here as species that have been recorded from only one or two countries) at a regional and local level (see Methods for explanation of formulae).

	Estimated using data from:		
	Mkomazi	CGH	Both sites
1. Revised genera, based on total known species			
No. undescribed species (=uK/k)	376	401	382
Total species	1219	1244	1225
Ratio Total/Known	1.4462	1.4762	1.4535
2. Revised genera, based on localized species			
No. undescribed species (=uL/l)	1566	313	772
Total species	2409	1156	1615
Ratio Total/Known	2.8577	1.3709	1.9160
Estimated total species in all genera ¹			
Based on (1) above	3089	3153	3105
Based on (2) above	6104	2928	4093
% new species or species currently at infraspecific rank ²			
Based on (1) above	44.8	45.9	45.1
Based on (2) above	72.1	41.8	58.3

¹ = (Total estimated revised species) \times (Total/Known). Total estimated revised species = 843 + 1293 = 2136 (See Tables 1 & 2).

² = ((Estimated - Known)/Estimated) \times 100. The number of known species = 1705.

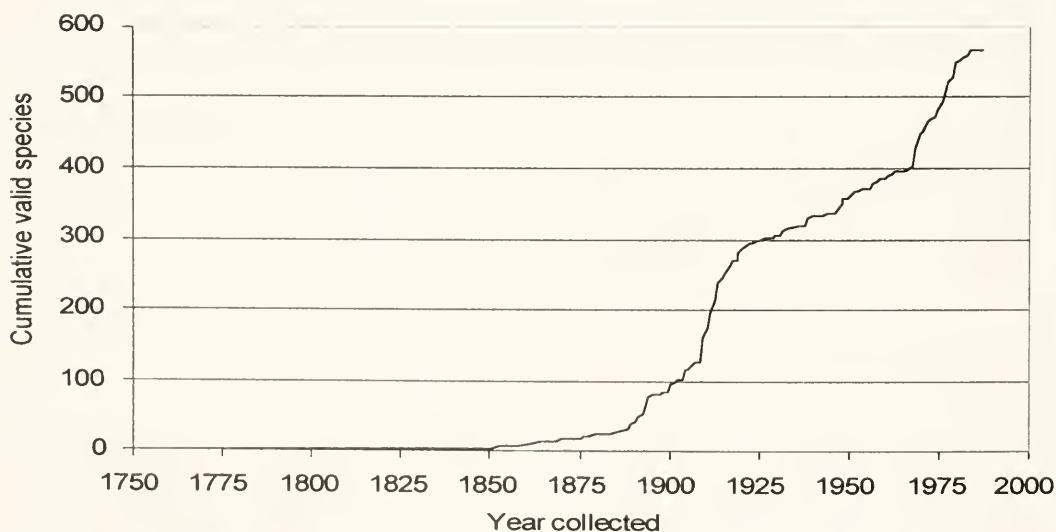


Fig. 1. Accumulation of new Afrotropical species in selected genera in relation to collection date of the type (publication date used where collection date absent). Information from Bolton (1974a, 1980, 1981a, 1981b, 1982, 1983, 1987). Only revisions from 1980 onwards included except for *Cataulacus* (Bolton 1974a) which was updated in the 1982 publication.

Table 5. Number of ant species revised and described by B. Bolton over a 16 year period (includes an extra year to account for the preparation time for the 1973 publications). Initial species refers to the number of valid species before the revision began. Average number initial species processed per year = $672/16 = 42$.

Year published	Initial species	No. new species	No. species after revision
1973	43	10	48
1974	29	7	33
1975	67	29	88
1976	63	14	72
1977	52	37	86
1978	0	0	0
1979	23	17	38
1980	102	63	176
1981	55	23	74
1982	87	16	81
1983	44	65	107
1984	0	1	1
1985	0	0	0
1986	0	0	0
1987	107	46	167
Total	672	328	971

there was a burst of collecting from 1910 to 1925, overlapping with the period when George Arnold was mainly active. Following this burst, species accumulation increased at a slower rate until the 1970's when a new generation of ant collectors started using collecting techniques such as pitfall trapping, tree fogging and Winkler bag leaf litter extractions that produced species that had previously gone undetected. These techniques are still yielding many new species and additional techniques such as soil sifting should start tapping into the subterranean species that are still poorly known.

Time taken to revise genera.—Over a 16-year period, Barry Bolton revised genera that initially contained a total of 672 species, amounting to processing 42 initial species per year (Table 5). The total of 971 species after revision amounts to describing and characterising a species every four working days. Over such a long period and taking into account other concerns and responsibilities, this is a formidable

rate of species processing that is unlikely to be equalled or bettered by anyone working at an equivalent level of thoroughness.

Based on Bolton's level of productivity, it would take about 21 years for one person to revise the remaining unrevised genera (Table 2). The genera *Camponotus*, *Cre-matogaster*, *Dorylus*, *Lepisiota*, *Pachycondyla* and *Pheidole* would each take more than a year to revise.

DISCUSSION

Afrotropical ant species richness.—The method presented here, that of excluding widespread species in calculating the proportion of new species, has not been presented before and is an attempt (following on Hodkinson and Hodkinson 1993) to address the problem of differences in the average geographical distribution of known and undescribed species. The estimate of 4093 Afrotropical ant species produced by using this method is 32% greater than the 3105 species estimated using the conventional ratio of undescribed to all known species. These estimates could be improved if more sites are included.

In total, therefore, 45–58% of species are undescribed or currently incorrectly placed at subspecific rank. This range of values compares favourably with the 52% unknown species, calculated from Hölldobler and Wilson's (1990) estimate of 20000 species world-wide and the actual number (at the end of 1993) of 9538 species determined by Bolton (1995a). Shattuck (1999) states that the Australian ant species diversity might well be double that currently known, which also matches the estimates presented here for the Afrotropical region. At a local level, Watt *et al.* (1997) estimated that 40% of the ants they captured in Mbalmayo Forest Reserve in southern Cameroon were undescribed which compares favourably with the 44–45% undescribed species for all

genera recorded at the two localities in the present study.

On the basis that 18% of the world's described ant species are found in the Afrotropical region (calculated from Bolton 1995a), the species diversity estimates presented here can be extrapolated to a world level to give an estimated world diversity of between 17250 and 22739 species. However, as the Nearctic and Palaearctic ant faunas are much better known than those from other regions, the 18% Afrotropical ant species is likely to be an underestimate.

Progress with sampling of ants in Africa.—Awareness about the threats to biodiversity have increased funding for inventory-based conservation research and as ants are a favoured indicator taxon (Andersen 1997), there has been a consequent tremendous recent growth in ant collections. Intensive sampling projects in the Afrotropical region include: Mbal Mayo Forest Reserve in southern Cameroon (Watt *et al.* 1997); coastal and interior forest in Gabon (Fisher, in prep.); Mkomazi Game Reserve in Tanzania (Robertson 1999); Cape of Good Hope, Robben Island, Brenton-On-Sea, Fairfield Farm near Napier, Kogelberg Biosphere Reserve, and other sites in the Cape fynbos, South Africa (Robertson and co-workers, in prep.); Cape indigenous evergreen forests (Fisher, in prep.); Mondi Estate in Kwazulu-Natal (Fisher, in prep.); and widespread pitfall trapping by E. Marais in Namibia. However, there are still enormous gaps in our coverage. Countries such as Angola, Mozambique, Malawi, Zambia, Central African Republic, Ethiopia and Sudan have yet to be sampled using modern inventory techniques. Even the best sampled countries such as South Africa and Zimbabwe remain patchily sampled and there is not one country in the Afrotropical region where ants have been sampled adequately in all major vegetation regions.

Future strategies for collecting.—The best approach to adequately sampling the ants

of a large area such as the Afrotropical region is through intensive inventory-based sampling of particular localities by general collecting and a combination of replicated pitfall trapping, Winkler bag leaf litter extractions, beating or sweeping of vegetation, chemical knockdown of arboreal fauna and soil sampling. The use of replicable sampling methods makes it possible to statistically compare sites using techniques described in Colwell & Coddington (1994) and Chazdon *et al.* (1998) and in this way to make scientifically based assessments of alpha, beta and gamma diversity. Fisher (1996, 1998, 1999) has pioneered this approach in Madagascar although only for leaf litter and ground fauna. Recent studies, still unpublished (e.g. Fisher and Robertson in prep. for a site near Ambositra in Madagascar), have used a wider range of replicated sampling techniques. Superficial general collecting of many localities is of more limited value than the inventory approach although it is useful for providing distributional data. As ants are dominant and ecologically important organisms in terrestrial ecosystems, growth of collections will also continue due to the submission of specimens by ecologists and agricultural researchers for identification by ant systematists.

Inventory-based assessments of areas for conservation using ants will ensure continued funding of scientifically-based ant collecting in the Afrotropical region, provided there remains backup by ant systematists. The areas to be sampled will be largely dictated by the conservation funding bodies and by the political stability of the areas that need assessment. Notwithstanding the political issues, the neglected countries such as those listed above, need attention. With this increased ant collecting, the need for more taxonomic work on ants will become all the more apparent.

Current progress with Afrotropical ant taxonomy.—Based on relative proportion of species, we are about 39% of the way

through revision of the Afrotropical ant genera to modern standards and to revise the remaining genera would take one person 21 years to complete at 'Bolton speed'.

On a world level, there are about 41 people currently working on the taxonomy of ants. Although this seems a large number, the productivity of most of these taxonomists is much less than that of B. Bolton and their work is often limited to regional faunas. In addition, a number of our key established 'global view' systematists have either recently retired or are about to retire. We could end up with a situation similar to that in termite taxonomy (Eggleton 1999) although we are likely to remain stronger in terms of number of systematists.

The low taxonomic productivity of most ant systematists can be attributed largely to their occupation with other endeavours: ecological and biological research on their study organisms, administration, contract identification work, computer programming, and teaching duties. Revising ant genera at the rate that B. Bolton has achieved is therefore rarely attained and for most systematists one would need to settle for a speed of revision at best half or even quarter of Bolton's rate. However, there is room for improvement and I feel that ant systematists need to prioritise alpha taxonomy and not let it take a back seat which seems to be increasingly the case.

Unlike the situation in North America, Europe, South America and Asia, there is only one resident ant systematist in Africa and hence progress with documenting Afrotropical ants will depend largely on the involvement of outside 'global-view' systematists working on taxa that are represented in the Afrotropical region.

Strategies for advancing Afrotropical ant taxonomy.—The two goals of a strategy to improve ant taxonomy are firstly, to ensure that the number of ant systematists does not dwindle but remains stable or grows and secondly, to improve the effec-

tiveness and productivity of current ant systematists. Regarding the first aspect, it is vital that the museums holding important ant collections are committed to employing ant systematists. It is remarkable that the most important ant collection in the world at the Harvard Museum of Comparative Zoology has no full-time ant systematist committed to alpha taxonomy and has a curator that can work only part-time on this vital collection. The Natural History Museum in London, with the second largest ant collection in the world, should continue its support of a position in ant systematics once the present incumbent retires. The South African Museum holds the largest ant collection in Africa and should also remain committed to supporting ant systematics, especially as it is important to maintain an ant identification service for applied entomologists in Africa.

Training is an important aspect of safeguarding the future body of ant systematists because filling of positions in systematics is usually controlled more by the quality of the candidate than by the group he/she works on. Hence, the contribution to training by ant systematists at universities is essential to the future growth of ant systematics.

Regarding the second component in the strategy, there are five ways in which the effectiveness and productivity of current ant systematists could be improved: (1) In order to cope with the conflict between projects geared to collection growth as opposed to taxonomic projects, we need to make the latter a priority and plan time to spend on them. For instance, university lecturers often find it easiest to plan time for taxonomic work over the long vacations. (2) Dedicated funding of ant taxonomic revisions along the same lines as the Australian Biological Resources funding for catalogues, in which money is allocated in proportion to the size of the taxon, would be ideal for improving goal-setting and productivity. In reality, this type

of funding is rare because a taxonomic revision does not answer applied problems directly. (3) A more realistic approach to obtaining funding for ant taxonomy would be to link it to more easily obtained funding for applied field-based projects. Funding from these projects can be used for employing and training parataxonomists for time-consuming sorting, mounting and curation of ants. Funding bodies should commit themselves to permitting a direct taxonomic component in the project so that there are funds to employ people to measure specimens and funds to visit overseas ant collections to examine types. Funding should also be built into these projects for storage and curation of the specimens. (4) There is a great need for training of, and exchange of ideas between, established ant systematists, especially the large number residing outside North America and Europe. Better communication via e-mail would help, but the funding of one or more training and planning meetings would be ideal. (5) As there is still so much work to be done in revising all Afrotropical ant genera (at least 21 man-years), it is important to prioritise groups for revision. In the Afrotropical region, the unrevised groups encountered most frequently when identifying ants are *Pheidole*, *Crematogaster* and *Camponotus*. These groups also happen to be among the most diverse of the unrevised genera (Table 2) and are also among the most difficult taxonomically, either because of worker polymorphism (*Pheidole* and *Camponotus*) or because of a paucity of external morphological species-discriminating characters (*Crematogaster*). Not surprisingly therefore, these groups have been avoided and to get them done quickly it would be best to develop a funded strategy.

Ants are an economically and ecologically important group in terrestrial ecosystems in the Afrotropical region and improving their taxonomy would in turn improve the networking of ecological, agri-

cultural and behavioural ant research. The present study provides the information for planning a funded strategy to document the Afrotropical ant fauna. The challenge is to create a synergy between the different role players (systematists, ecologists, funding bodies) so that individual efforts are not swamped by the immensity of the job at hand.

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On the Identity of *Pheidole vaslitii* Pergande (Hymenoptera: Formicidae), a Neglected Ant from Baja California

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Abstract.—The ant *Pheidole vaslitii* Pergande has remained a taxonomic enigma since its description over a hundred years ago from a series of workers collected in the Sierra San Lazaro, Baja California Sur, Mexico. A reexamination of the apparent type series in the USNM collection reveals that some of the specimens—including a major worker designated as “lectotype” by Creighton (1958)—are not true types and are not conspecific with *P. vaslitii*. Selection of a new lectotype of *P. vaslitii* secures its identity as a form closely related to *P. hyatti*. It differs from “typical” *P. hyatti* by the presence of more extensive sculpture on the head of the major and minor workers and by its shorter body appendages, but intermediate phenotypes occur in parts of Baja California and California. Based on current evidence *P. hyatti* is reasonably interpreted as a single, polytypic species, with both *P. vaslitii* and an infraspecific name—*P. hyatti solitanea* Wheeler, described from Point Loma, California—as newly recognized **junior synonyms**.

In 1896 Pergande described a number of new ant taxa from northwestern Mexico, based on collections made by Eisen and Vaslit during a California Academy of Sciences expedition to the region (Pergande 1896). Most of the new ants were from Tepic in the state of Nayarit, but a few species had been collected in the Cape Region of Baja California. The taxonomic status of most of these named forms has long since been resolved, but one of the species from Baja California—*Pheidole vaslitii*—has suffered an ongoing identity crisis. Despite pronouncements on *P. vaslitii* by Forel (1901), Wheeler (1914), and Creighton (1958), its taxonomic status—whether it represents a distinct species or is a junior synonym—has never been satisfactorily determined. Creighton (1958) actually complicated the situation by designating as the “lectotype” of *P. vaslitii* a major worker that was not part of the series on which Pergande’s original description was based. In preparing a checklist of the ants of Baja California (Johnson and Ward, in prep.) it became necessary to determine

the relationship of *P. vaslitii* to other named taxa, and to deal with the consequences of Creighton’s (1958) actions. It will be argued that Creighton’s lectotype designation was invalid and that it inappropriately tied the name “*Pheidole vaslitii*” to a mainland Mexican species not found in Baja California. True *P. vaslitii* appears to be a geographical variant of the widespread species *Pheidole hyatti* Emery.

MATERIALS AND METHODS

Specimens belonging to the original type series of *Pheidole vaslitii* were examined from holdings of the California Academy of Sciences, San Francisco (CASC) and the Smithsonian Institution, Washington, DC (USNM). Other relevant material in the genus *Pheidole* was studied in those two collections and in the following: Natural History Museum of Los Angeles County (LACM), California Department of Food and Agriculture, Sacramento (CDAE), Bohart Museum of Entomology, University of California at Davis (UCDC), and Robert A. Johnson collection, Tempe,

Arizona (RAJC). Other collection abbreviations cited in the text are: AMNH (American Museum of Natural History, New York), MCSN (Museo Civico di Storia Naturale, Genoa) and MCZC (Museum of Comparative Zoology, Harvard University).

All measurements were taken at 50 \times using a Wild M5A microscope and a Nikon stage micrometer, and are presented here in millimeters to two decimal places. The following measurements and indices were used:

HW	Head width: maximum width of the head, as seen in full-face (frontal) view, excluding the eyes.
HL	Head length: length of the head, measured in full-face view, from the anterior clypeal margin to the midpoint of a line drawn across the posterior margin.
EL	Eye length: length of the eye, measured with the head in full-face view.
SL	Scape length: chord length of the scape, from the base (excluding the neck) to the apex; this measurement was taken by positioning the scape so that both ends lay in the same focal plane.
BSW	Basal scape width: maximum measurable width of the basal third of the scape (measured in major workers only).
PrW	Pronotum width: maximum width of the pronotum, measured in dorsal view.
LHT	Length of the metatibia (hind tibia): length of the metatibia measured in lateral view from the distal extremity to the proximal end, excluding the medial lobe of the articulation with the femur (see Ward 1989, fig. 5).
CI	Cephalic index: HW/HL
SI	Scape index: SL/HW
REL	Relative eye length: EL/HL

REL2 Relative eye length, using HW: EL/HW

HTI Metatibial index: LHT/HW

The following index of pilosity was employed:

HTC Metatibial setal count: number of standing hairs, i.e., those forming an angle of 45 $^{\circ}$ or more with the cuticular surface (Wilson 1955), visible in outline on the outer (extensor) surface of the metatibia. This count was taken with the line of view orthogonal to the plane of tibial flexion.

TAXONOMIC HISTORY OF *PHEIDOLE VASLITII*

Pergande (1896: 883) described *Pheidole vaslitii* from specimens collected by Eisen and Vaslit in the Sierra San Lazaro, Baja California Sur, in September 1894. The original series of twenty-two specimens was said to comprise nine major workers (or "soldiers") and thirteen minor workers ("workers"). In the same paper Pergande described several other *Pheidole* taxa, including one which he thought was related to *P. vaslitii* and which he named *Pheidole obtusospinosa* (Pergande 1896: 889). This latter species was from Tepic, Nayarit, however, and the description was based on a large series ("many specimens") of major workers only. *Pheidole obtusospinosa* was synonymized with *P. vaslitii* by Forel (1901: 430). Wheeler (1914) established, however, that *P. obtusospinosa* was the same as *P. subdentata* Pergande (1896), also described from Tepic, but based on minor workers only. By this time it was also clear that, unlike most *Pheidole* species, the major workers of *P. subdentata* are quite variable in size. Wheeler treated *P. subdentata* as a subspecies of *P. vaslitii*, a situation that continued until 1958 when Creighton assigned it species rank. Until recently this species has gone by the name *P. subdentata* Pergande, with *P. obtusospinosa* as a junior synonym, but Bolton (1995) pointed out

that Pergande's *subdentata* is preoccupied (it is a secondary junior homonym of *Oecophthora subdentata* Mayr 1853). *P. obtusopinosus* is the first available replacement name for the species described from Tepic, Nayarit.

In the meantime the problem of the identity of *Pheidole vaslitii* was addressed by Creighton (1958) who examined Pergande's type series in the USNM. He concluded that type series comprised more than one species, with most of the major workers—and all of those that matched Pergande's (1896) description of the *P. vaslitii* major—being *Pheidole cockerelli* Wheeler (1908). The minor workers were said to be a mix of *Pheidole crassicornis tetra* Creighton (1950) and *P. hyatti* Emery (1895). Concerned about the replacement of *P. cockerelli* or *P. crassicornis tetra* by a more obscure senior synonym, Creighton chose as a lectotype of *P. vaslitii* a major worker that did not correspond to Pergande's (1896) original description. In fact, the identity and labeling of the specimen designated as "lectotype" indicate that it was not part of the original type series of *P. vaslitii* (see below). Moreover, Creighton (1958) admitted that he could not say what species, if any, the "lectotype" represented, i.e., he could not determine whether it belonged to any previously described species of *Pheidole*, except that it was not the species whose major worker was described by Pergande (1896) as *P. vaslitii*. This was the last action taken on *P. vaslitii* whose identity has thus remained in limbo for the last 40 years.

Other *Pheidole* names associated at various times with *P. vaslitii* are (1) *P. hirtula* Forel (1899), originally described as a variety of *P. vaslitii*, but later raised to species by Creighton (1958); (2) *P. arizonica* Santschi (1911), described as such, but treated as a variety of *P. vaslitii subdentata* by Wheeler (1914) and as a subspecies of *P. vaslitii* by Creighton (1950), before being synonymized under *P. subdentata* Pergande (Creighton 1958); and (3) *P. acolhua*

Wheeler (1914), originally described as a variety of *P. vaslitii*, but later synonymized under *P. hirtula* (Creighton 1958).

REEXAMINATION OF THE TYPE SERIES

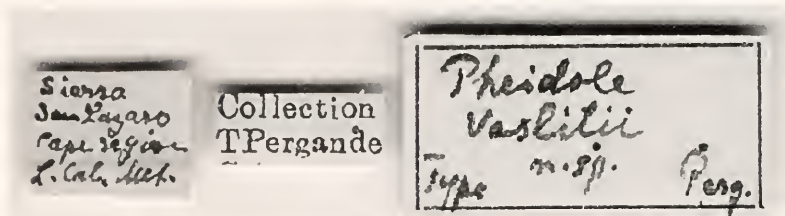
Syntypes true and false

The solution to the *Pheidole vaslitii* problem lies in a careful analysis of the type specimens. In the USNM there are 14 specimens that appear, at first glance, to be part of the original type series. These specimens can be divided into two subsets (see also Creighton 1958: 208).

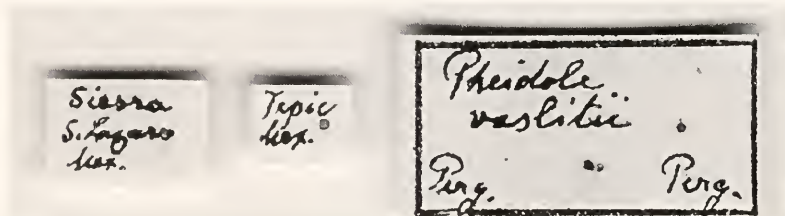
Subset A comprises 11 specimens (4 major workers, 7 minor workers) each on their own pin and bearing two sets of labels (Fig. 1): (1) Pergande's handwritten locality label "Sierra/San Lazaro/Cape region/L. Cal. Mex.", and (2) a printed label "Collection/T Pergande". Two specimens (one major and one minor worker) additionally bear a third, black-bordered label with the following notation in Pergande's hand: "*Pheidole vaslitii*/n. sp./Type Perg.". On the label of the minor worker "n. sp." is placed in parentheses. As Creighton (1958) noted, the ink on the handwritten labels has faded to brown and the paper has yellowed. The major workers and most of the minor workers agree closely with Pergande's (1896) original description of *P. vaslitii*.

Subset B consists of two major workers and one minor worker whose labeling is rather different (Fig. 2). The locality labels are handwritten, evidently by Pergande, in a black ink which has not, to this day, faded, and the label paper has not yellowed in color like that of subset A. The locality for the two majors is given as "Sierra/S. Lazaro/Mex." and for the minor "Tepic/Mex.". All three specimens bear a red USNM type label as follows: "Type/No. 4488/U.S.N.M.", with the number handwritten and the remaining text printed. One of the major workers also has a third label in Pergande's writing: "Phei-

1



2



Figs. 1–2. 1, Sample of labels from specimens in “subset A” of the apparent type series of *Pheidole vaslitii*. The type label is from one of the major workers. See text for further details. 2, Sample of labels from specimens in “subset B” of the apparent type series of *P. vaslitii*. The identification label is from one of the major workers. All three specimens of “subset B” also bear a red USNM type label with the number “4488”. See text for further details.

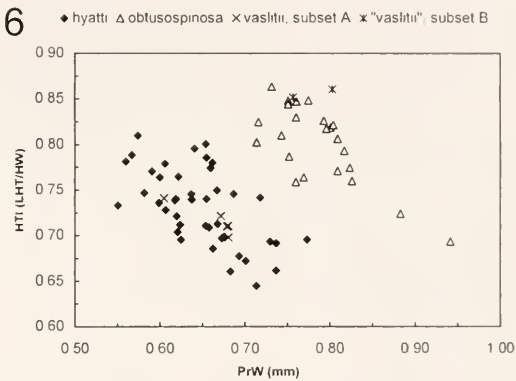
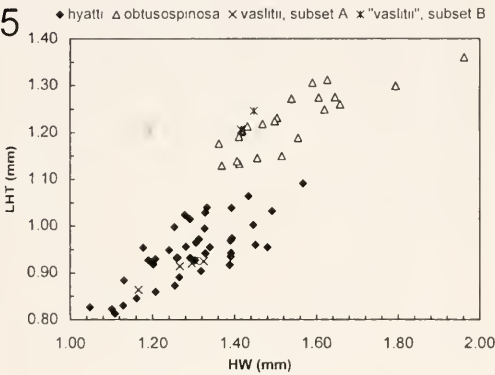
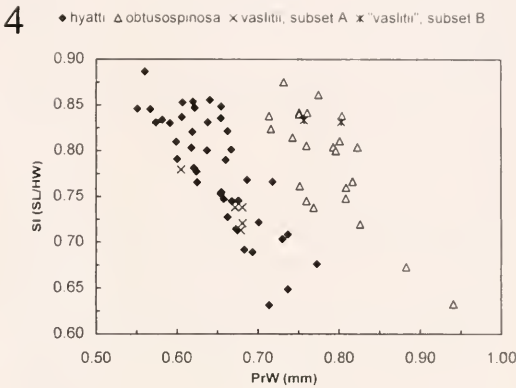
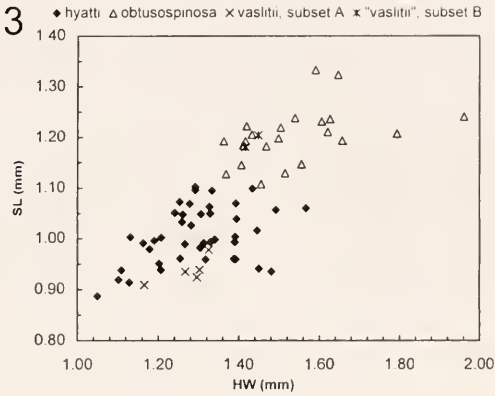
dole/*vaslitii*/Perg. Perg.”. It is this specimen that Creighton (1958) designated as the lectotype of *P. vaslitii*. None of these three “type” specimens matches the original description of *P. vaslitii*.

In discussing the different appearance of the labels Creighton (1958: 209) surmised that Pergande had rewritten those of subset B when designating the specimens as types: “Dr. Smith informs me that Pergande noted in the type book of the National Museum that he had marked three specimens of *vasliti* as types. It would appear that when he did so he altered the locality labels of these three specimens, probably because he realized that the original labels were not holding up as well as might have been wished”.

Creighton (1958) did not mention—and perhaps did not examine—the minor worker from Tepic, but he freely admitted that the two major workers were not part of the series on which Pergande based his description of *P. vaslitii*: “They may be medias of a polymorphic species related to

subdentata or the majors of a dimorphic one related to *hyatti*. But there is no doubt about one thing: neither of them contributed anything to Pergande’s description of the major of *vasliti*” (Creighton 1958: 210). As mentioned above, Creighton’s choice of a lectotype that did not correspond to the species described by Pergande was motivated by a desire to maintain nomenclatural stability: Creighton concluded that the species represented in subset A (i.e., the probable true syntypes of *P. vaslitii*) included *P. cockerelli* and *P. crassicornis tetra* and he did not want to see one of these younger (and better known) names relegated to synonymy.

Insofar as the designated specimen was not a syntype of *P. vaslitii*, Creighton’s (1958) choice of lectotype is invalid (ICZN, Article 74.2). Further evidence that his “lectotype” was not part of the original type series of *P. vaslitii* comes from consideration of the identity of the three specimens in subset B (Figs. 3–6): all three are *Pheidole obtusospinosa* Pergande, a species



Figs. 3–6. Bivariate plots of various measurements and indices in major workers of *Pheidole obtusospinosa* and *P. hyatti*. Note that the *P. vaslitii* types from “subset A” fall within the values for *P. hyatti*, while those of “subset B” correspond to *P. obtusospinosa*. The plots exclude “supermajors” of *P. obtusospinosa* (HW > 2.20).

which is widespread in adjacent mainland Mexico but which is not known to occur in Baja California. In the course of studying the ant fauna of Baja California I have examined many hundreds of specimens of *Pheidole* in various collections (CASC, CDAE, LACM, RAJC, UCDC, USNM). None of the Baja specimens belonged to *P. obtusospinosa*, although I encountered examples of this distinctive species from Sonora, Sinaloa, Nayarit, Jalisco, and Arizona. In fact, the two major workers of subset B agree very closely with a series of seventeen *P. obtusospinosa* majors from Tepic, Nayarit (collected by Eisen and Vaslit), which had been placed under *P. vaslitii* in the USNM collection. Given that this arrangement of specimens was due to

Pergande, it indicates that he confused the two species.

I conclude that Pergande’s marking of the three specimens in subset B as “types” of *P. vaslitii* occurred after the original description of that species, and that it involved the mislabeling of *P. obtusospinosa* specimens collected at Tepic, Nayarit. That Pergande was less than careful in these matters is indicated by the fact that in his original description of *Pheidole granulata* he cites the type locality as Tepic (Pergande 1896: 891), although the type specimens were actually from San José del Cabo, Baja California Sur (Gregg 1969: 101). Removing the *P. obtusospinosa* specimens from consideration as valid types of *P. vaslitii*, we can refocus our attention on

subset A which, it seems clear, contains the true syntypes.

A study of the USNM specimens in subset A indicates that the following two species are involved:

1. A *Pheidole* species conspecific with, or closely related to, *P. hyatti*. This is represented by four major workers and four minor workers. The majors were misidentified by Creighton (1958) as *P. cockerelli*, while he identified the minors as *P. hyatti*. In the collection of the California Academy of Sciences (CASC) there are two additional *P. vaslitii* syntypes (one major worker, one minor) that belong to this species. They both bear faded labels "Sierra/San Lazaro" and "Pergande/Type", in Pergande's handwriting.
2. A second species of *Pheidole*, related to *P. crassicornis* Emery, represented by three minor workers. These were identified by Creighton (1958) as *P. crassicornis tetra*.

Designation of a new lectotype

Given that subset A (in the USNM) and the two CASC specimens are part of the actual type series of *P. vaslitii* it is proper that the lectotype be chosen from among them. Of the two species present in the type series, only one is represented by major workers, so I have chosen as the lectotype of *P. vaslitii* one of the major workers in the USNM series. This particular specimen (with HW 1.32, HL 1.40, SL 0.98, LHT 0.92) also bears the old faded "Pheidole/vaslitii/n. sp./Type Perg." label. Formal lectotype designation is indicated below under "Taxonomic summary".

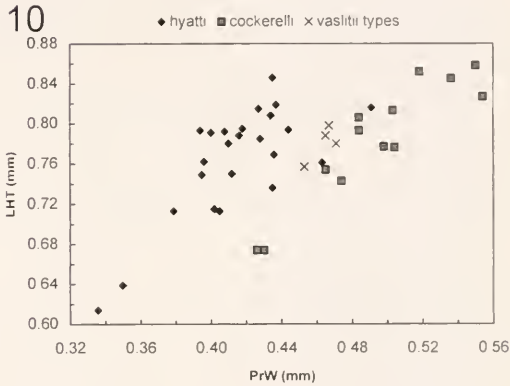
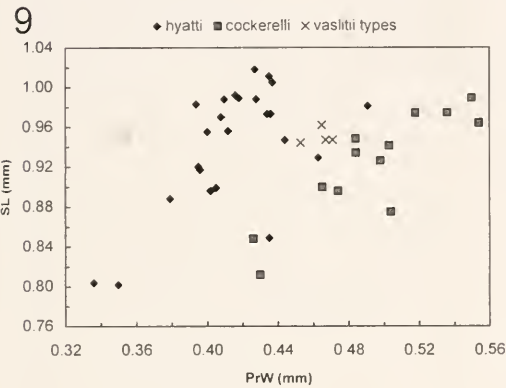
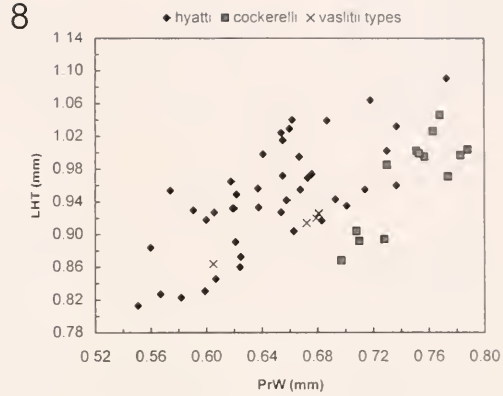
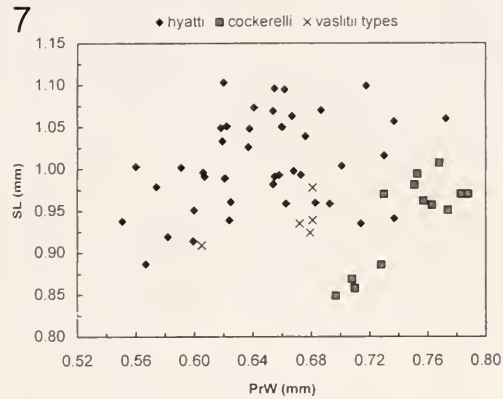
The paralectotypes in USNM and CASC are then as follows: (1) four major workers (three in USNM, one in CASC) and five minor workers (four in USNM, one in CASC) conspecific with the lectotype, and (2) three minor workers (in USNM) not conspecific with the lectotype; these are discussed further below in the section en-

titled "Identity of the second species in the type series". Specifically *excluded* from the paralectotype series are the three workers of *P. obtusospinosa* (subset B).

With this action taken, the identity of *P. vaslitii* becomes linked with the question of the magnitude and nature of geographical variation in *Pheidole hyatti*, a species widespread in the southwestern United States and northern Mexico.

Relationship of *Pheidole vaslitii* to *P. hyatti*

The major workers of *P. vaslitii* agree well with *P. hyatti* majors from other parts of Baja California and southwestern United States. They have the base of the scape strongly bent and flattened (BSW/SL 0.12–0.14); the ventrolateral hypostomal teeth are well developed and spine-like, and displaced laterally about 0.8 times the distance from the midline to the dorsolateral hypostomal teeth; the posterior margin of the head is deeply impressed medially, and this impression continues on the dorsum of the head as a narrow, transversely rugulose, median furrow which changes to a broader smooth, shiny strip above the frontal triangle; the mesonotum is angular in lateral profile; the propodeal spines are short, stout, and erect; the petiolar node is narrowly transverse; and the postpetiole is about 1.6 times broader than long, with obtuse, blunt lateral angles (as seen in dorsal view). Body sculpture is like that of *P. hyatti*, with the mesosoma largely foveolate and subopaque, the sculpture weakening medially and on the side of the pronotum; irregular transverse carinulae occur on the anterior portion of the pronotum. The head dimensions (HW 1.17–1.32, HL 1.25–1.40, CI 0.93–0.95), and relative lengths of the scapes (SL/PrW 1.36–1.50) and legs (LHT/PrW 1.35–1.43) fall within the values of *P. hyatti* and, in the case of the last two indices, largely outside those of *P. cockerelli* (see also Figs. 7–8). The body pilosity is relatively long and fine-tipped, not blunt-tipped as in *P.*



Figs. 7–10. Bivariate plots of various measurements and indices in major workers (Figs. 7–8) and minor workers (Figs. 9–10) of *Pheidole hyatti* and *P. cockerelli*. The *P. vaslitii* types (subset A) lie closer to the cloud of points representing *P. hyatti*.

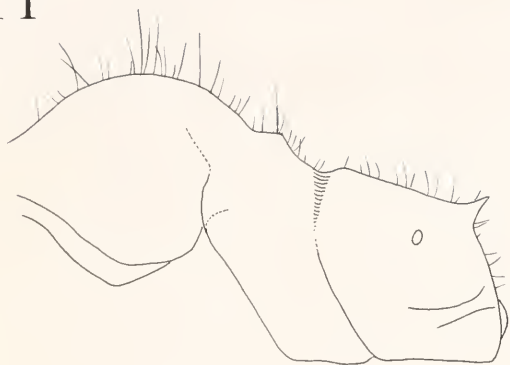
cockerelli (compare Figs. 12 and 13), and the tibiae are conspicuously hirsute (HTC 19–22, compared with HTC 1–17 in *P. cockerelli*).

It may be that Creighton (1958) mistook these *P. vaslitii* majors for *P. cockerelli* because the head sculpture is denser than is typical for *P. hyatti*. Fine reticulate-foveolate sculpture extends to the posterolateral corners of the head so that the occipital lobes (normally shiny in *P. hyatti*) are dulled. Rugoreticulum extends more than half the distance from the upper margin of the compound eye to the occipital lobes. But the rugoreticulum is not as well developed as in the majors of *P. cockerelli*, where it essentially covers the occipital lobes. Differences between *P. cockerelli* and

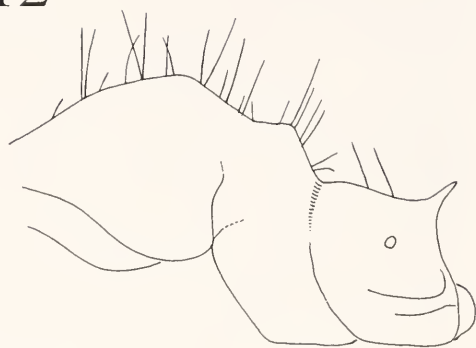
P. vaslitii in pilosity, scape length, and leg length are also evident, and with respect to these characters the *P. vaslitii* types fall within the orbit of *P. hyatti* (Figs. 7–8, 13–14, 17–18).

The conspecific minor workers (4w in USNM, 1w in CASC) agree with *P. hyatti* minors from other localities, although they tend to exhibit more extensive foveolate sculpture on the head. This character varies widely, however, and when considering *P. hyatti* minors from throughout the range of this species one finds all degrees of variation from an almost entirely smooth, shiny head (except between the compound eye and antennal insertions) to one dulled by extensive foveolate sculpture on all regions except medially. The *P.*

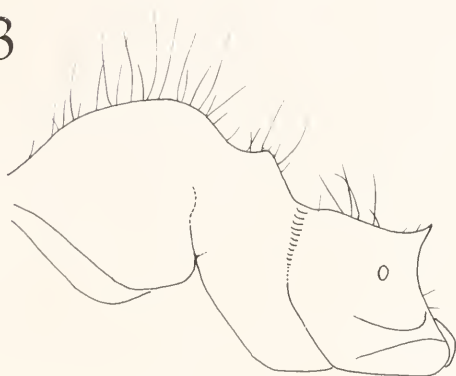
11



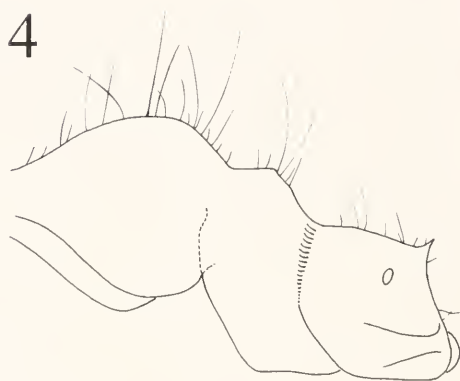
12



13



14



15



16



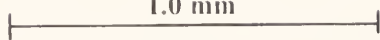
17



18



1.0 mm



Figs. 11-18. *Pheidole* major workers, lateral views of the mesosoma (11-14) and anterior views of the metatibia (15-18). Pilosity shown in outline only. 11, 15, *P. obtusospinosa* (Tepic, Nayarit); 12, 16, *P. cockerelli* (Yavapai Co., Arizona); 13, 17, *P. hyatti* (*P. vasilii* paralectotype from Sierra San Lazaro, BCS); 14, 18, *P. hyatti* (Riverside Co., California).

vaslitii workers lack the weak rugoreticulum that typically occurs on the posterior portions of the head in minors of *P. cockerelli*. The pilosity on these *P. vaslitii* minor workers is also more slender and flexuous than that of *P. cockerelli*. The tibial pilosity is conspicuous (HTC 14–19), like that of *P. hyatti*. Measurements and indices are well within the limits of *P. hyatti*: HW 0.63–0.66, CI 0.82–0.84, SI 1.44–1.49, SL/PrW 2.01–2.08, REL 0.23–0.24, HTI 1.19–1.22, LHT 0.76–0.80, LHT/PrW 1.66–1.72 ($n = 4$ for the first six sets of values, because one of the USNM specimens is headless) (see also Figs. 9–10).

Thus, *Pheidole vaslitii* falls within the range of variability that occurs in the widespread species, *P. hyatti*. In addition to denser head sculpture, the *P. vaslitii* types also tend to have shorter scapes and legs than *P. hyatti* from other regions (Figs. 3–10). The differences are not diagnostic, however, and individuals intermediate in morphology between *P. vaslitii* and more “typical” *P. hyatti* occur widely, especially on the Baja California peninsula and in California. It is possible that there is more than one biological species in this complex, but I can find no consistent phenotypic discontinuities that would justify recognition of more than one taxon. Without a more detailed (preferably genetic) analysis of the situation, it seems advisable to treat *P. hyatti* as a single polytypic species, with *P. vaslitii* as its junior synonym. This is formally indicated below (under “Taxonomic summary”), along with the overdue synonymy of *P. hyatti solitanea* Wheeler under *P. hyatti*.

While it may be coincidental, it seems worth noting that other *Pheidole* species in Baja California show some evidence of north-south clines in the intensity of head sculpture. This is seen most strikingly in *Pheidole yaqui* Creighton and Gregg: populations of this species from California and northern Baja California have the posterior portion of the head of the major worker largely smooth and shining, while

populations from farther south on the peninsula show increasing development of transverse rugulation on the posterior margin of the head (Ward, pers. obs.).

Identity of the second species in the type series

Three minor workers from the syntype series of *P. vaslitii* belong to a distinctly different species. The head is broader (HW 0.66–0.68, CI 0.88–0.90), and the scapes and legs are shorter (SI 1.18–1.21, HTI 1.00–1.02). The head is sublucid, with weak reticulate-foveolate sculpture overlain by irregular longitudinal carinulae; the sculpture is less developed medially where there are more extensive shiny interspaces. The standing pilosity is short, sparse and blunt, with about 7–9 standing hairs visible in profile on the mesosoma dorsum, and none on the extensor surface of the tibiae.

Creighton (1958) identified these workers as *Pheidole crassicornis tetra* Creighton. He actually cited the author as W. M. Wheeler (1908), but the name *tetra* did not become available until 1950 when Creighton raised Wheeler’s infrasubspecific name to subspecies rank (Bolton 1995). In the literature *tetra* has continued to be treated as a subspecies of *P. crassicornis*. Naves (1985) opined that it was a distinct species, similar to *P. diversipilosa* Wheeler (1908), whereas Creighton (1950) emphasized the existence of intermediates and considered all three names to refer to a single species.

The three minor workers from Baja California evidently belong to what could be called the *P. crassicornis* complex. In comparison with minor workers from Arizona and Texas, provisionally identified as *P. diversipilosa* and *P. crassicornis tetra* respectively, the Baja minors agree closely in overall habitus, pilosity and body measurements, but differ by having more conspicuous longitudinal carinulae on the head, greater encroachment of reticulate-foveolate sculpture on the center of the

pronotum, and slightly longer legs (LHT 0.66–0.70, HTI 1.00–1.02; compared with LHT 0.53–0.62 and HTI 0.89–0.97 in the Arizona and Texas material). With respect to pilosity they are most similar to the Arizona specimens, both having slightly shorter hairs than the Texas workers. In the Baja workers the length of the longest seta on the petiole is 0.090–0.104 mm, on the postpetiole 0.094–0.105 mm, and on abdominal tergite IV 0.081–0.096 mm. In the absence of any associated major workers—and given continued uncertainty about the relationship of *crassicornis*, *tetra* and *diversipilosa* to one another—it does not seem feasible to identify the minor workers any further at this time.

TAXONOMIC SUMMARY

Pheidole hyatti Emery 1895

(Figs. 13, 14, 17, 18)

Pheidole hyatti Emery 1895. Syntype workers (majors, minors), San Jacinto, California (E. Hyatt) (AMNH, MCSN).

Pheidole vaslitii Pergande 1896. Syntype workers, Sierra San Lazaro, Baja California Sur, Mexico (Eisen & Vaslit) (CASC: 1 major worker, 1 minor worker; USNM: 4 major workers, 4 minor workers); one major worker in USNM here designated **lectotype** to clarify application of the name *P. vaslilli* (see previous discussion on page 90). **Syn. nov.**

Pheidole hyatti var. *ccitonodora* Wheeler 1908. Syntype workers (majors, minors), Texas, New Mexico, Colorado (AMNH, LACM, MCZC). Synonymy by Creighton (1950: 180).

Pheidole hyatti subsp. *solitanea* Wheeler 1915. Syntype workers (majors, minors), queens, Point Loma, San Diego, California (W. M. Wheeler; P. Leonard) (AMNH, MCZC). **Syn. nov.** Synonymy previously listed in a report by Snelling and George (1979: 104), not considered a formal publication by Bolton (1995).

P. cockerelli; Creighton (1958), misidentification of *P. vaslitii* syntypes (part)

Diagnosis, major worker.—Medium-sized (HW 1.05–1.57; HL 1.14–1.63, LHT 0.81–1.09; $n = 47$); scape conspicuously flattened and bent basally (BSW/SL 0.09–0.15), of

moderate length (SI 0.63–0.89, SL/PrW 1.28–1.79), not exceeding the posterior margin of the head when laid back against the head; ventral hypostomal teeth well-developed, spine-like, much closer to the dorsolateral hypostomal teeth than to the midline; posterior margin of head with deep median impression; eyes of moderate size, REL 0.15–0.19; pronotal humeri not prominent; mesonotum distinctly angular in profile; propodeal spines short, stout and directed posterodorsally; postpetiole with blunt, obtuse lateral angles (dorsal view); legs relatively long, HTI 0.64–0.81, LHT/PrW 1.30–1.66. Anterolateral regions of head with rugoreticulate and reticulate-foveolate sculpture which variably invades the medial and posterior portions of head (a smooth, shiny area generally persists in the medial impression above the frontal triangle); posterior margin of head finely sculptured or smooth, lacking conspicuous rugoreticulum; mesosoma mostly foveolate and (sub)opaque, becoming sublucid on the side of the pronotum and on the pronotal dorsum, where there are usually transverse carinulae. Body pilosity abundant, long, slender, fine-tipped; conspicuous on the tibiae (HTC 15–27). Color variable, from light orange-brown to dark reddish-brown, gaster often darker than the rest of body.

Comments.—*P. hyatti* is found from Texas, Oklahoma and Colorado west to Nevada and California and south into northern Mexico (Kempf 1972; Smith 1979). As befits its wide distribution, the species occupies a broad range of habitats including Chihuahuan, Sonoran and Great Basin deserts, short-grass prairie, pinyon-juniper woodland, oak woodland, riparian woodland, chaparral, and coastal sage scrub (Droual 1983; Gregg 1963; Snelling and George 1979; Suarez *et al.* 1998; Wheeler and Wheeler 1973, 1986). With respect to foraging behavior, *P. hyatti* appears to be a generalist omnivore rather than a seed-harvesting specialist (Wheeler 1908; Snelling and George 1979). Colonies of *P. hyatti* are

frequently subject to raids of the army ant, *Neivamyrmex nigrescens* (Droual and Topoff 1981; Mirenda *et al.* 1980; Ward 1999).

***Pheidole obtusospinosa* Pergande 1896**
(Figs. 11, 15)

Pheidole obtusospinosa Pergande 1896. Syntype workers (majors), Tepic, Nayarit (Eisen & Vaslit) (LACM, USNM).

Pheidole subdentata Pergande 1896. Syntype workers (minors), Tepic, Nayarit (Eisen & Vaslit) (LACM, USNM). Note: Wheeler (1914) synonymized *P. obtusospinosa* under *P. subdentata*, but Pergande's *P. subdentata* is preoccupied (Bolton 1995), so *P. obtusospinosa* is the first available replacement name.

Pheidole vaslitii; Creighton (1958), misidentification and invalid "lectotype" designation.

Diagnosis, major worker.—Large species, variable in size (HW 1.36–2.90, HL 1.39–2.55, LHT 1.13–1.50; $n = 28$); in medium-sized workers (HW < 2.20) scape relatively long (SI 0.63–0.88, SL/PrW 1.32–1.66) and bent basally but usually not conspicuously broadened (BSW/SL 0.07–0.10); in supermajors (HW > 2.20) scape relatively short (SI 0.44–0.48, SL/PrW 1.00–1.13) and basal portion notably broadened (BSW/SL ~ 0.14); ventral hypostomal teeth present, generally spine-like, much closer to the dorsolateral hypostomal teeth than to the midline; posterior margin of head with shallow, obtuse V-shaped impression, becoming more deeply notched in supermajors (HW > 2.20); eyes relatively small, REL 0.11–0.16; pronotal humeri not strongly protuberant; mesonotum bluntly angular in profile; propodeal spines short, stout and directed posterodorsally; postpetiole with blunt, obtuse lateral angles (dorsal view), more prominent in supermajors; legs long, HTI 0.52–0.86, LHT/PrW 1.19–1.62 (in all but supermajors HTI 0.69–0.86, LHT/PrW 1.45–1.62). Upper surface of mandibles smooth and shiny, except for weak basal striae. Dorsum of head largely covered with rugoreticulate and reticulate-foveolate sculpture, densest (and the longitudinal orientation of the ru-

gulae least evident) in supermajors; mesosoma mostly foveolate and (sub)opaque, becoming sublucid on the side of the pronotum and on the pronotal dorsum, where there are transverse carinulae. Body pilosity very abundant, shorter and more blunt-tipped than in *P. hyatti*, conspicuous on the tibiae (HTC 25–36). Color varying from orange-brown to dark reddish-brown, the gaster sometimes darker than the rest of the body.

Comments.—*P. obtusospinosa* is known from Arizona, Sonora, Sinaloa, Nayarit and Jalisco. Creighton (1958) recorded the species, under the name *P. subdentata*, from "elevations up to 6300 feet in many of the mountains of southern Arizona" and noted that "while the number of *subdentata* nests in an area is often quite large, this species never seems to exclude other ants from such areas". In Arizona I have encountered *P. obtusospinosa* in oak-pine-juniper woodland and oak-juniper woodland, at elevations ranging from 1670m to 2100m. Colonies were found nesting under stones, and workers (including soldiers) foraged nocturnally on the ground, and came to tuna fish baits. Groups of minor and major workers were also seen, without brood, under a rotting log and in a dead branch of *Quercus grisea*. There are recent records of *P. obtusospinosa* workers (mostly minors) visiting extrafloral nectaries of *Ferocactus*, *Opuntia* and *Pachycereus* at several sites near Punta Chueca, Sonora (leg. Kevin Walker).

***Pheidole* sp. (*crassicornis* complex)**

Pheidole vaslitii Pergande 1896 (part); 3 minor workers, Sierra San Lazaro, Baja California Sur, Mexico (Eisen & Vaslit) (USNM); not conspecific with the above newly-designated lectotype of *P. vaslitii*.

Pheidole crassicornis tetra; Creighton (1958).

Comments.—The identity of the three minor workers is discussed above. Based on material from southern United States the major workers of this complex may be recognized by the following features (1)

ventrolateral hypostomal teeth well developed, spine-like, displaced laterally about 0.75 times the distance from the midline to the dorsolateral teeth, (2) base of scape flattened and broadened ($BSW/SL \sim 0.14$), (3) scapes very short, $SI < 0.60$, $SL/$

$PrW < 1.16$, (4) legs very short, $HTI < 0.62$, $LHT/PrW < 1.18$, (5) standing pilosity blunt-tipped, sparse on appendages, $HTC < 10$, (6) posterior third of head largely smooth and shining, lacking reticulate-foveolate sculpture.

KEY TO SPECIES ASSOCIATED WITH THE NAME "*PHEIDOLE VASLITII*"

The following key is not intended to be comprehensive. It is concerned only with those *Pheidole* species that have been confused with *Pheidole vaslitii*, and is presented as a summary of the differences between them. Most of these species belong to the *P. fallax* group, as defined by E. O. Wilson in his forthcoming monograph on the New World *Pheidole* (Wilson, in prep.). Wilson recognizes a separate *P. crassicornis* group that seems likely to be nested phylogenetically within the *P. fallax* group, insofar as it possesses the basic features of the latter group but manifested as more derived states. The term "*P. crassicornis* complex", as used below, refers to three taxa in the *P. crassicornis* group (*P. crassicornis*, *P. crassicornis tetra*, and *P. diversipilosa*) whose relationships to one another need further clarification.

Pheidole obtusospinosa and *P. hirtula* are very closely related. The distinctions cited in the key to majors are taken from Creighton (1958), and are admittedly slight. Future study may well show that these two taxa are simply geographical variants of a single species. I have been unable to find diagnostic differences between the minor workers of *P. obtusospinosa* and *P. hirtula*.

Major workers

- 1 Legs relatively long, $LHT\ 1.11\text{--}1.50$, and eyes small ($EL/LHT\ 0.16\text{--}0.21$); major workers variable in size ($HW\ 1.31\text{--}3.07$), and "supermajors" ($HW > 2.20$) occur; body pilosity conspicuous, relatively short and dense (Figs. 11, 15), $HTC\ 25\text{--}48$ 2
- 1' Legs shorter, $LHT < 1.10$, and eyes relatively large ($EL/LHT\ 0.22\text{--}0.29$); major workers less variable in size ($HW\ 1.05\text{--}1.57$), supermajors lacking; body pilosity variable (Figs. 12–14, 16–18), generally less abundant, $HTC\ 0\text{--}27$ 3
- 2 In largest individuals ($HW > 2.50$) head strongly cordate, conspicuously narrowed towards the mandibular insertions (Creighton 1958, fig. 1); rugulate sculpture tending to be less developed on posterior half of head, which may be subclucid (northeastern Mexico, west to Chihuahua, Durango and Jalisco) *hirtula* Forel
- 2' In largest individuals ($HW > 2.50$), head less strongly cordate, less strikingly narrowed anteriorly (Creighton 1958, fig. 2); posterior half of head with rugulate and reticulate-foveolate sculpture tending to be more strongly developed (Arizona, Sonora, Sinaloa, Nayarit, Jalisco) *obtusospinosa* Pergande
- 3 Scapes and legs very short, $SL/PrW < 1.16$, $LHT/PrW < 1.18$; standing pilosity sparse, $HTC < 10$ (southern United States, northern Mexico) *crassicornis* complex
- 3' Scapes and legs longer, $SL/PrW\ 1.21\text{--}1.79$, $LHT/PrW\ 1.23\text{--}1.66$; pilosity variable 4
- 4 Pilosity long, fine-tipped, and abundant (Figs. 13–14, 17–18), $HTC\ 15\text{--}27$; occipital lobes varying from smooth and shiny to reticulate-foveolate and opaque, but lacking conspicuous rugoreticulum; scapes and legs longer, $SL/PrW\ 1.28\text{--}1.79$, $LHT/PrW\ 1.30\text{--}1.66$ ($n = 47$) (see also Figs. 7–8), (southwestern United States, northern Mexico) *hyatti* Emery
- 4' Pilosity shorter, blunt-tipped and less dense (Figs. 12, 16), $HTC\ 1\text{--}17$; occipital lobes rugoreticulate and subopaque; appendages shorter, on average; $SL/PrW\ 1.21\text{--}1.33$, $LHT/$

PrW 1.23–1.36 (n = 13) (see also Figs. 7–8) (southwestern United States, northern Mexico)
 *cockerelli* Wheeler

Minor workers

- 1 Legs long, LHT 0.85–0.95, and eyes small (EL/LHT 0.19–0.23); body pilosity abundant and moderately long, HTC 14–28 *hirtula* Forel and *obtusospinosa* Pergande
- 1' Legs shorter, LHT 0.52–0.85, and eyes relatively large (EL/LHT 0.22–0.29); body pilosity variable, often less abundant, HTC 0–24 3
- 2 Scapes and legs very short, SI 1.11–1.22, HTI 0.89–1.02 (n = 11); eyes smaller, REL2 0.23–0.27; pilosity sparse and short, HTC 0–7 *crassicornis* complex
- 2' Scapes and legs longer, SI 1.24–1.71, HTI 1.07–1.38 (n = 41); eyes larger, REL2 0.27–0.34; pilosity longer and more abundant, HTC 7–24 3
- 3 Pilosity on body and appendages long, fine-tipped, and abundant, HTC 11–24; upper third of head smooth and shiny or partially invaded by foveolate sculpture and subopaque, but lacking rugulae; head more elongate (CI 0.77–0.85), scapes and legs longer, SL/PrW 1.95–2.50, LHT/PrW 1.64–2.01 (n = 28) *hyatti* Emery
- 3' Pilosity less common, blunt-tipped, HTC 7–18; upper third of head largely opaque, covered with foveolate sculpture and overlain by weak rugoreticulum or longitudinal rugulation; head broader (CI 0.82–0.90) and appendages shorter, on average, SL/PrW 1.74–1.99, LHT/PrW 1.49–1.67 (n = 13) *cockerelli* Wheeler

CONCLUDING REMARKS

The “*Pheidole vaslitii* problem” exemplifies two difficulties that have often arisen in ant taxonomy: insufficient access to, or analysis of, type specimens on the one hand, and yet (paradoxically) a subtle typological bias on the other hand, which has sometimes led investigators to overrate the significance of differences among populations of the same species. It is ironical that Creighton’s (1958) dubious choice for the lectotype of *P. vaslitii* would not have occurred if he had recognized the major workers in the type series as variants of the older-named *Pheidole hyatti*, in which the “typically” smooth shiny occipital lobes had become clouded by sculpture. To be fair, it could be argued that Creighton did not possess a sufficiently large and geographically extensive series of specimens of *P. hyatti*, especially from Baja California. From the vantage point of the more extensive data now available *Pheidole hyatti* appears to be a classic example of a polytypic species (Mayr 1982),

i.e., one that consists of a series of geographically dispersed and morphologically disparate populations, linked together by intermediate populations and showing evidence of recent or ongoing gene flow. At the same time, the possibility cannot be excluded that one or more cryptic species lurks within this complex of populations, especially in view of the broad range of habitats occupied.

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***Bassus macadamiae* sp. n. (Hymenoptera: Braconidae: Agathidinae),
Parasitoid of *Ecdytolopha torticornis* and *E. aurantianum*
(Lepidoptera: Tortricidae) in Macadamia Nut Crops in Central and
South America**

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Abstract.—*Bassus macadamiae* Briceño and Sharkey, sp. n. is described and illustrated. Specimens of *B. macadamiae* are solitary internal parasitoids of larvae of the tortricid moth *Ecdytolopha torticornis* (Meyrick) and *E. aurantianum* (Lima), insect pests of macadamia crops, *Macadamia integrifolia* Maiden & Botche, in Central and South America.

Ecdytolopha torticornis (Meyrick) and *E. aurantianum* (Lima) (Lepidoptera: Tortricidae) are pests of the macadamia nut, *Macadamia integrifolia* Maiden & Botche (Fam. Proteaceae), in Central and South America (Arizaleta and Diaz 1995, Badilla 1996). Lara (1987) reviewed the economic importance of *Ecdytolopha torticornis* in Costa Rica, and reported damage of 16%. Blanco *et al.* (1993) reported infestation rates in Costa Rica of 12–39% for hulls, and 1–7% for nuts. In Venezuela, Arizaleta *et al.*, (1997) reported *E. aurantianum* as the main pest attacking macadamia crops, but no studies have been conducted to ascertain damage levels.

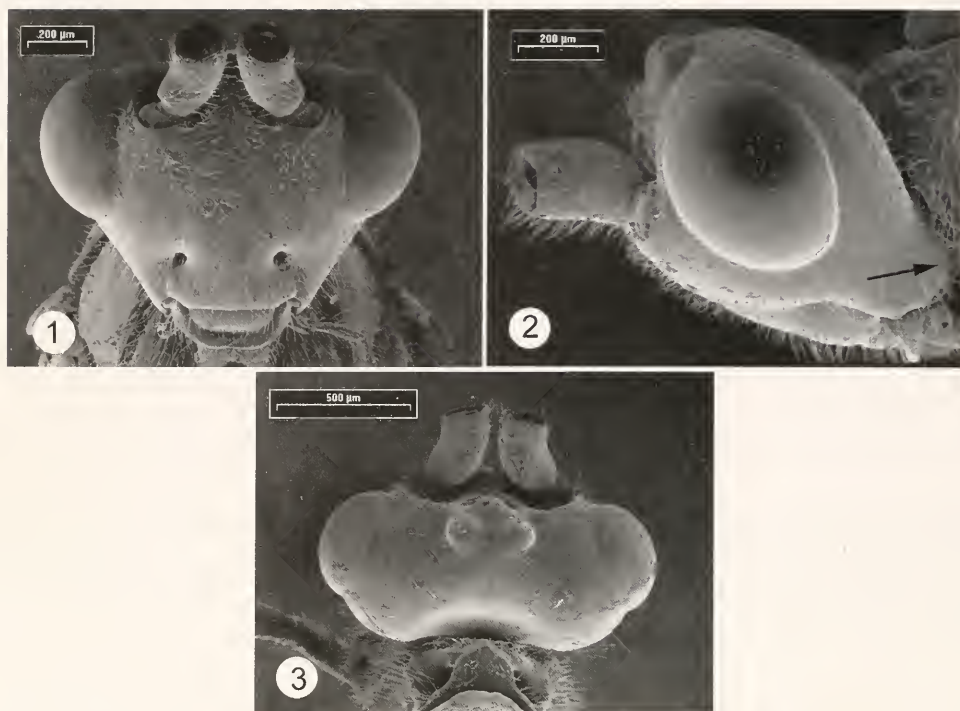
Larvae of *Ecdytolopha torticornis* and *E. aurantianum* feed mainly in the mesocarp and endocarp of the nuts. Blanco *et al.* (1993) reported three braconid wasps parasitizing larvae of *E. torticornis* in Costa Rica, i.e., two *Apanteles* spp. and one *Ascogaster* sp. Specimens of an undescribed species of *Bassus* have been reared from larvae of *E. torticornis* and *E. aurantianum*, attacking young nuts of macadamia in Costa Rica and Venezuela (Arizaleta and

Díaz 1995, as *Agathis* sp.) and due to its economic importance we feel that a formal name for the parasitoid is useful.

MATERIALS AND METHODS

The terminology for wing venation follows Sharkey and Wharton (1997). Other terminology follows Chou and Sharkey (1989). Abbreviations for insect collections are as follows:

- UCOB: Museo Entomológico "José Manuel Osorio" at the Universidad Centroccidental "Lisandro Alvarado" in Barquisimeto, Venezuela.
- UCR: Insect Collection of the Universidad de Costa Rica, San José, Costa Rica.
- MIZA: Museo del Instituto de Zoología Agrícola "Francisco Fernández Yépez", Universidad Central de Venezuela, Maracay, Venezuela.
- UK: Insect Collection of the Department of Entomology, University of Kentucky, Lexington, Kentucky, USA.



Figs. 1-3. *Bassus macadamiae*: 1, head frontal view; 2, head lateral view; 3, head dorsal view.

***Bassus macadamiae* Briceño & Sharkey
sp. n.**

(Figs. 1-10)

Holotype female.—(numbers in parenthesis refer to ranges found in the 14 specimens comprising the type series). *Length*: Body 5.6 mm (4.4-6.8), antenna 4.7 mm (3.9-5.7), forewing 5.1 mm (4.1-5.8), ovipositor sheath 5.0 mm (4.0-5.5). *Head* (Figs. 1-3): Vertex sparsely minutely punctate; distance between lateral ocelli 0.5 (0.46-0.60) times ocello-ocular distance

and 1.2 (1.0-1.5) times diameter of median ocellus; frons sparsely minutely punctate; frontal depression moderately deep; antenna with 35 (34-36) flagellomeres; scape 1.3 (1.1-1.5) times as long as wide; face 1.5 (1.4-1.6) times as wide as eye height and 0.6 (0.56-0.6) times as wide as head; face and clypeus sparsely minutely punctate; face 0.85 (0.7-0.9) times as high as wide; tentorio-ocular line 0.93 (0.63-0.93) times inter-tentorial line; malar space 2.7 (2.2-3.0) times basal width of mandible and 0.62 (0.48-0.68) times eye height; temple, in dorsal view, evenly curved; ridge between antenna absent; gena rounded posteroventrally. *Mesosoma* (Figs. 4-8): Pronotum sparsely minutely punctate; notaulus complete and smooth; scutellar furrow smooth, without carinae; scutellum weakly punctate, without apical carina; posterior semicircular depression of scutellum present; posterior surface of scutellum punctate; propleuron without distinct bump; mesopleuron mostly smooth,

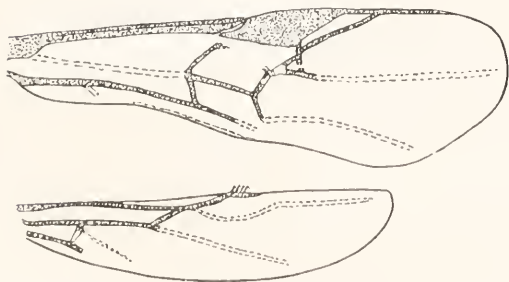
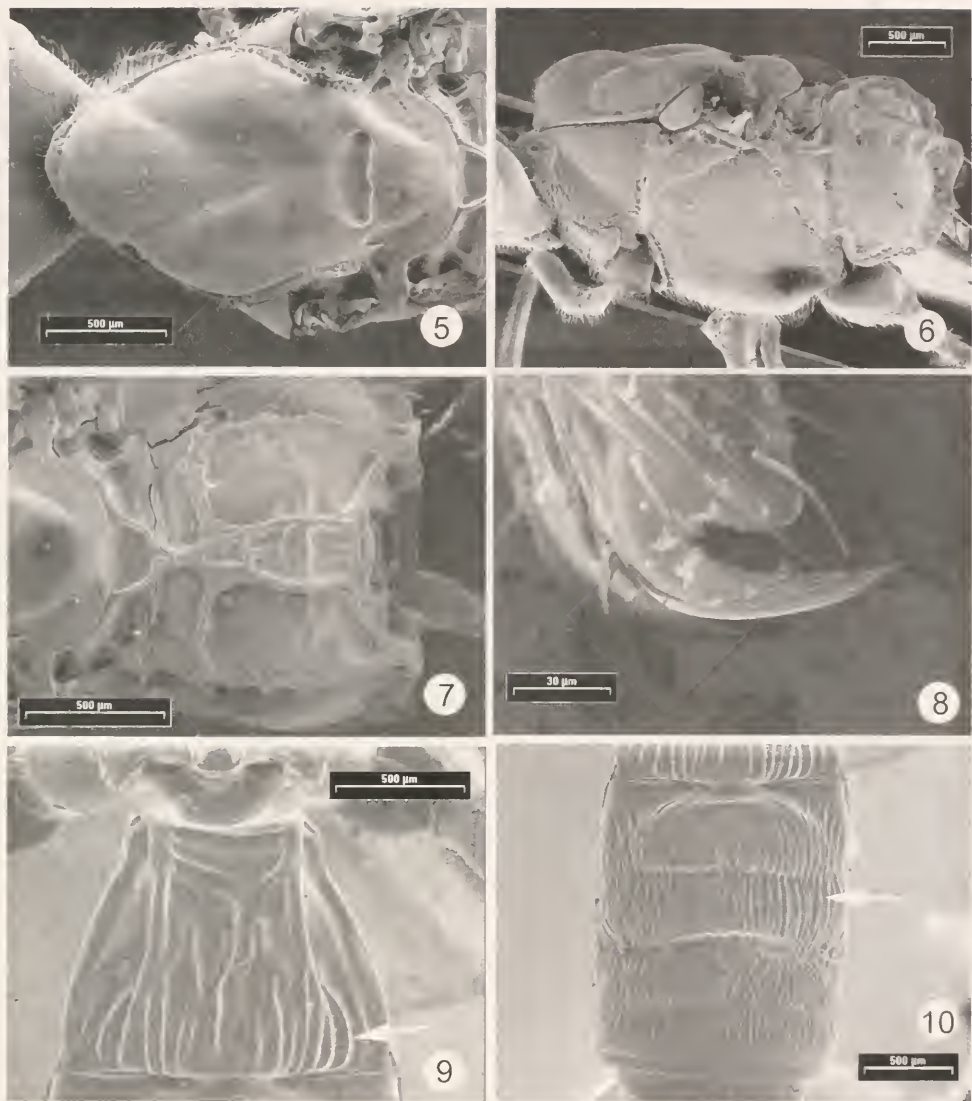


Fig. 4. *Bassus macadamiae*: wings.



Figs. 5–10. *Bassus macadamiae*: 5, dorsal view of mesosoma; 6, lateral view of mesosoma; 7, propodeum; 8, tarsal claw; 9, dorsal view of first metasomal tergum; 10, dorsal view of second and third metasomal terga.

weakly punctate on margins, with posterior margin carinate; sternaulus distinct, with deep posterior depression; metapleuron sparsely minutely punctate, rugulose ventrally; propodeum carinate with two distinct median longitudinal carinae and two distinct lateral longitudinal carinae; anterior median areola and posterior median areola present; anterior transverse carina present; propodeal pseudosternite with strong transverse ridge; hind coxal

cavity separated from metasomal foramen by wide and well developed sclerite; forewing 3.1 (3.0–3.6) times as long as wide; vein 1cu-a of forewing postfurcal; 2nd submarginal cell of forewing (1RS) triangular and petiolate, i.e., 2RS and r-m veins fused anteriorly; RS of forewing almost straight; midtibia with 7 (7–9) spines; medial midtibial spur 0.44 (0.36–0.55) times length of basitarsomere; hind femur 3.1 (2.6–3.2) times longer than wide; medial

hind tibial spur 0.43 (0.36–0.47) times as long as basitarsomere; tarsal claws simple with a right-angled basal lobe. *Metasoma* (Figs. 9–10): First median tergite costate, 0.91 (0.81–0.92) times as long as wide apically; second median tergite costate 0.4 (0.27–0.4) times as long as wide, with semicircular transverse groove; third median tergite costate, 0.29 (0.23–0.3) times as long as wide, with semicircular transverse groove; ovipositor sheath 1.05 (0.8–1.2) times as long as forewing. *Color*: Mostly reddish orange. Head, including antenna, dark brown; clypeus and mouthparts light brown; maxillary and labial palpi yellow; pronotum and mesonotum dark brown; metanotum, propodeum and metasoma red to orange; fore and hind tarsus yellow, remainder dark brown; hind coxa red to orange, remainder dark brown; wings hyaline with weak infuscation; stigma and veins dark brown; ovipositor sheath melan.

Male.—Essentially as in female.

Diagnosis.—Members of the new species may be distinguished from all other New World species of *Bassus* by the following combination of characters: first three metasomal medial tergites costate; propodeal pseudosternite with a strong transverse carina; hind tibia with 14–18 spines; ovipositor sheath about as long as the forewing.

Material examined.—*Holotype female*: VENEZUELA, Villanueva, Lara; 1200m; VII-1993 (F. Díaz) (UCOB). *Paratypes*: COSTA RICA: 1 Female, 1 male, Limón, Siquirres, 03-VI-1995 (UCR). 3 females, Turrialba, Cartago, 650 m, 29-VI-1996 (UCR). VENEZUELA, Lara: 3 females, Villanueva, 1200m, VII-1993 (F. Díaz) (UCOB) (MIZA). 1 male, Villanueva, 1200 m, III-1993, (F. Díaz) (UCOB). 1 Female, 2 males, Villanueva, 1200 m, 02-II-1995, (F. Díaz) (UCOB) (UK). 1 Female, Villanueva, 1200 m, 11-XI-97 (R. Paz) (UCOB).

Host.—Larvae of *Ecdytolopha torticornis* and *E. aurantium*. Females of *B. macadamiae* attack first instar larvae of both

hosts before they penetrate the nut. The parasitoid larva develops until the host leaves the nut to prepare to pupate. The parasitoid then emerges from the host and weaves a white cocoon on the external surface of the nut inside the hull.

Etymology.—The specific name *macadamiae* refers to the name of the host plant *Macadamia integrifolia*.

Remarks.—The genus *Bassus* lacks any apparent autapomorphy. At least, we know of none and none has been offered in the literature. The Microdini, to which *Bassus* belongs (Sharkey 1992), is an assemblage of mostly monophyletic genera. However, *Bassus* itself is probably rendered paraphyletic by the recognition of most or all of these genera. It will take a more quantitative approach to test this thesis.

Bassus macadamiae belongs to a species group of *Bassus* that illustrates this paraphyly problem. Members of this species group share a few putative synapomorphies such as longitudinal costae on metasomal terga one, two, and three, and a strong transverse ridge of the propodeal pseudosternite (area between the hind legs). These same characters are found in members of the genus *Braunsia* Kriechbaumer. On this limited evidence, and lacking contrary hypotheses supported with character state evidence, it seems that *Braunsia* s.l. and this species group of *Bassus* are more closely related to each other than members of the species group are to other species presently placed within the concept of *Bassus*. The distribution of the species group is cosmopolitan with the relative species abundance being greater in northern temperate regions. The similarities between species of *Braunsia* and members of this species group have never been noted in the literature but they are obvious enough to have induced Enderlein to describe some members of this species group of *Bassus* in *Braunsia*; *Bassus ochracea* (Enderlein) is one example. The species group includes, *Bassus ater* (Chou and

Sharkey), *B. ebulus* (Nixon), *B. atripes* (Cresson) and *B. calcaratus* (Cresson).

As it is presently defined, *Braunsia* is restricted to the Old World and appears to be monophyletic. Including the species described here in *Braunsia* would drastically expand the concept of the genus and, in our view, this generic reappraisal should only be done in the context of a more complete cladistic analysis. Here we take a conservative approach in applying the name *Bassus* to the new species.

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A New Genus, and First Host Records, for the Adeshini: Parasitoids of Hispine Beetles (Braconidae: Braconinae; Coleoptera: Chrysomelidae)

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Abstract.—The new genus *Aneuradesha* Quicke is described with its type species *A. harleyi* Quicke. This new species is a parasitoid of the hispine beetle, *Asmangulia cuspidata* Maulik, a pest of sugarcane and rice in India and Indonesia. In addition, we report that in insular Malaysia *Adesha albolineata* Cameron is a parasitoid of another hispine beetle, *Promecotheca cumingi* Baly, a pest of coconut palm. These are the first two host records for the braconine tribe Adeshini and strongly suggest that adeshines are specialist parasitoids of hispines.

Adeshini are a small, entirely tropical tribe of the large braconid wasp subfamily Braconinae, occurring in the Afrotropical, Oriental, Indo-Australian and Australian regions. They are known from only seven described species belonging to five genera (Achterberg 1983; Quicke 1986, 1988; Quicke & Ingram 1993), and the majority of these are known from only one or a few specimens. Until now, nothing was known about their biology, though many small tropical braconines are parasitoids of either leafminers, stem borers, or gall forming insects. Here we present the first host records for the tribe, based on two species, and describe a very distinctive new genus and species.

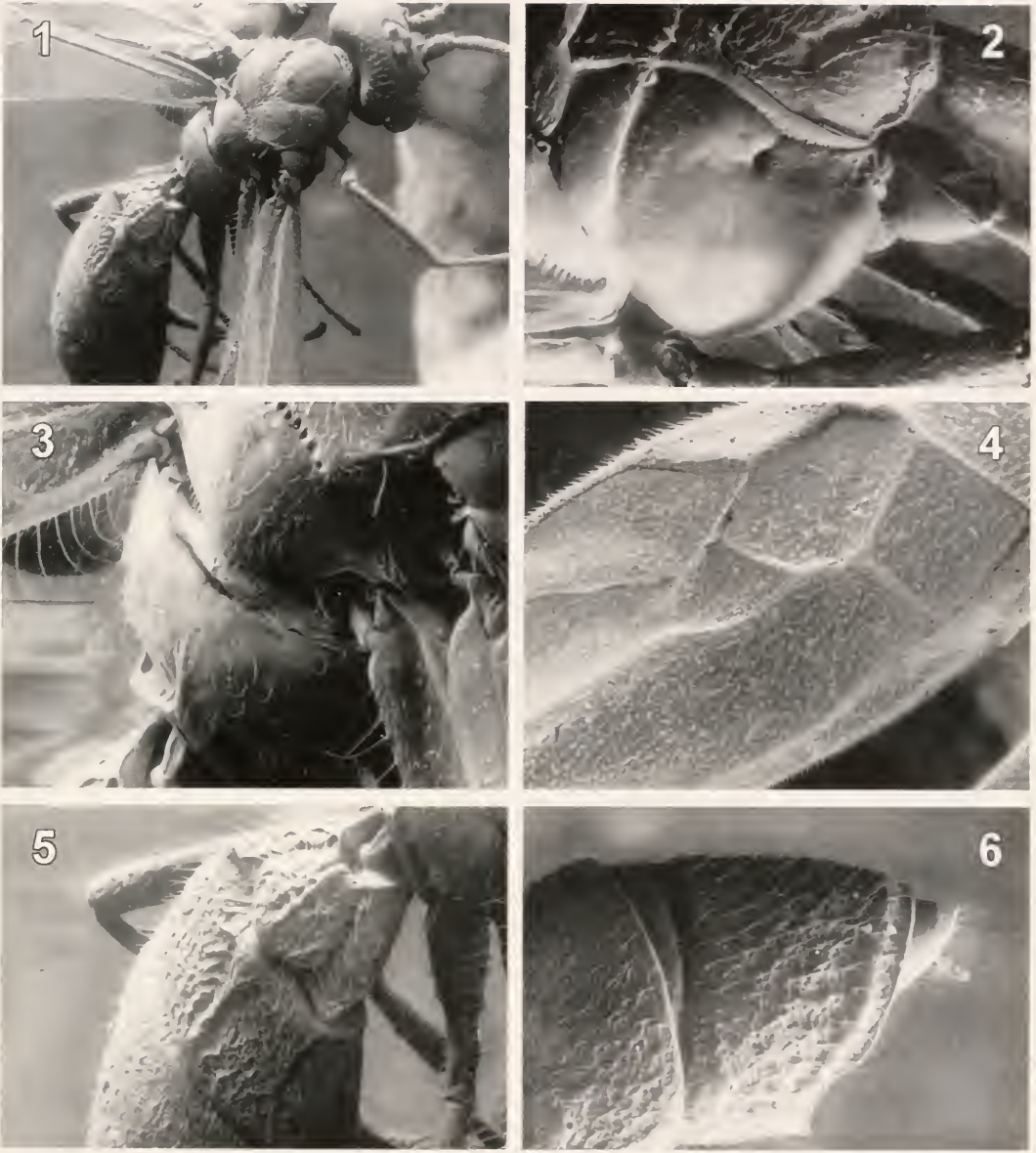
Terminology follows Wharton *et al.* (1997).

Aneuradesha Quicke gen. nov.

Diagnosis.—*Aneuradesha* can be distinguished from all other known genera of Adeshini by the complete absence of fore wing vein 2cu-a (Fig. 4; = vein CU1b in terminology of van Achterberg 1983), and also by the incomplete midlongitudinal

carina of the propodeum (Fig. 3). Members of the Adeshini can be recognised by fore wing vein 2CU arising at the same level as 1CU (Achterberg 1983; Quicke 1987).

Description.—Terminal flagellomere elongate, pointed but not acuminate. All flagellomeres much longer than wide; basal ones apically oblique. Face smooth and shiny. Hypoclypeus not strongly recessed into hypoclypeal depression. Eyes closest together below middle. Mesoscutum smooth and shiny, without a deep midlongitudinal groove (Fig. 1). Notauli deeply impressed, meeting at posterior third of mesoscutum where they form a weakly depressed punctate area (Fig. 1). Mesopleuron smooth, largely glabrous (Fig. 2). Middle lobe of metanotum without a midlongitudinal carina. Propodeum with an incomplete, midlongitudinal carina (Fig. 3). 2nd submarginal cell short, vein 2RS about as long as 3RSa. 2nd metasomal tergite with a distinct small midbasal area produced into a narrow midlongitudinal ridge (Fig. 5). 2nd metasomal suture narrow and crenulate.



Figs. 1-6. Environment chamber scanning electron micrographs of *Aneuradesha harleyi* gen. et sp. nov., male holotype: 1, habitus. 2, metapleuron. 3, scutellum to propodeum. 4, fore wing. 5, metasomal tergites 1-3. 6, lateral view of 5th metasomal tergite showing posterolateral emargination.

Type species.—*Aneuradesha harleyi* Quicke sp. n. by monotypy and original designation.

Remarks.—The complete lack of fore wing vein CU1b and the reduced propodeal carina are both probably autapomorphies of *Aneuradesha* with respect to the other genera of Adeshini.

Aneuradesha harleyi Quicke sp. nov.
(Figs 1-6)

Type material.—Male holotype: INDIA: Muzzafarnagar, 8.vi.1998, Atar Singh, ex *Asmangulia cuspidata*, IIE 23897 (BMNH). Male paratype (BMNH): same data as holotype.

Antenna with 34 flagellomeres. Height of clypeus (excluding hypoclypeus): intertentorial distance:tentorio-ocular distance = 1.0:3.7:2.0. Height of eye:width of head across eyes: width of face = 1.0:2.6:1.4. Transverse diameter of posterior ocellus: distance between posterior ocelli:shortest distance between posterior ocellus and eye = 1.0:1.2:2.2. Mesosoma 1.2 times longer than maximum height. Mesoscutum (Fig. 1) smooth except for punctures at bases of setae; moderately densely setose except the mid-longitudinal part of the middle lobe. Scutellar sulcus finely crenulate. Scutellum with a weak but distinct pit. Propodeum (Fig. 3) crenulate posteriorly. Posterior margin of hind wing weakly emarginate. Lengths of veins 2RS:3RSa:r-m = 1.3:1.28:1.0. Lengths of veins r:3RSa:3RSb = 1:1.45:5.75. Lengths of veins (Rs + M)b:2M = 1.0:1.55. Fore wing vein 1cu-a marginally postfurcal. Vein 2-1A tubular for approximately half length of 1st subdiscal cell. Base of hind wing evenly setose. Apex of vein C + SC + R with one especially thickened bristle (basal hamulus). Lengths of hind femur (excluding trochantellus): tibia:basitarsus = 2.0:3.3:1.0. First and 2nd metasomal tergites rugose with overlying granulose sculpture; more posterior tergites granulose superimposed on weak foveate sculpture. Posterior margin of 5th tergite with a distinct, transverse subposterior groove (Fig. 6).

Uniformly honey-yellow except for the flagellomeres, an ill-defined mark on the raised median area of the 1st metasomal tergite and a mark medio-basally on the 2nd metasomal tergite, which are blackish.

Biologies of *Adesha Albolineata* and *Aneuradesha Harleyi*

Aneuradesha harleyi is so far known only from the hispine chrysomelid beetle *Asmangulia cuspidata* Maulik, a leafminer pest of sugarcane and rice in India and Indonesia. Anwar (1944) records a "*Microbracon*" sp. as an ectoparasitoid of *A. cuspidata* larvae causing up to 38% parasitisa-

tion. Since, to our knowledge, no other braconid has ever been recorded from *A. cuspidata*, it is conceivable that "*Microbracon*" represents a misidentification of the species treated here as *A. harleyi*.

The authors recently had the opportunity to examine material of another parasitoid of a hispine, *Promecotheca cumingi* Baly, a pest of coconut palm in south and southeast Asia (Gallego *et al.* 1983; Mathur *et al.* 1984). A series of 12 specimens, sent to the second author for identification, turned out to belong to the type species of the type genus of Adeshini, *Adesha albolineata* Cameron (see van Achterberg 1983, for a redescription of *Adesha albolineata*, and Quicke, 1986, for a key to species of *Adesha*). Previously, *Adesha* had been recorded from Borneo and the Malay Peninsula, and *A. albolineata* was known only from two specimens. According to the collector, *A. albolineata* is an ectoparasitoid of larvae of *P. cumingi*. There appears, therefore, to be a very reasonable basis for considering Adeshini as specialist ectoparasitoids of hispine larvae.

Adesha albolineata: Material Examined: 5♀5♂ MALAYSIA: Sarawak, Buntal ex *Promecotheca cumingi* on Nipah (*Cocos nucifera*) 20.v.1998 (Drahman coll.); 1♀ same data except 17.ii.1998, IIE 23809/ S132 (all specimens in The Natural History Museum, London).

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Microgastrine (Hymenoptera: Braconidae) Parasitoids of *Colias lesbia* (Fabricius) (Lepidoptera: Pieridae)

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Abstract.—The microgastrine (Braconidae) parasitoids of *Colias lesbia* (Fabricius), a lepidopteran pest of alfalfa in southern temperate regions of South America, are reviewed. Three species, *Cotesia ayerza* (Brèthes), *C. glomerata* (Linnaeus) and *C. lesbiae* (Blanchard) are recognized and the morphological differences between them are presented. A lectotype for *C. ayerza* is designated.

Colias lesbia (Fabricius) is a lepidopteran pest of alfalfa, and is widespread in the southern temperate regions of South America. Throughout its range, it is attacked by three microgastrine (Braconidae) parasitoids. The taxonomy and identification of these parasitoids, which are all members of the genus *Cotesia*, have been problematic, with between two and five species being recognized in the complex. The purpose of this paper is to resolve these problems and to present morphological characteristics to distinguish between the species of *Cotesia* that attack *Colias lesbia*.

The subfamily Microgastrinae is cosmopolitan and contains thousands of species (Shenefelt 1972). They are internal parasitoids of larval Lepidoptera and are important in the natural and manipulated control of many pest species. The genus *Cotesia* contains hundreds of species that have been formally described, but even more that have not yet been described. The genus is also cosmopolitan and may be distinguished from all other Microgastrinae by the sculpture and shape of the first metasomal tergum and by the short ovipositor of females (cf. Mason 1981).

Shenefelt (1972, 1980) lists three species of Microgastrinae as parasitoids of *Colias*

lesbia, viz., *Cotesia glomerata* (Linnaeus), *C. ayerza* (Brèthes), and *C. lesbiae* (Blanchard) (all as *Apanteles*). There are other microgastrine names recorded as parasitoids of *Colias lesbia*; however, owing to well-researched synonymies (cf. Shenefelt 1972), only these three remain current in the literature.

Syntypes of *C. ayerza* were borrowed from the Museo Argentino de Ciencias Naturales and specimens of *C. lesbiae* determined by both Blanchard and Brèthes were borrowed from the Museo de La Plata. The type of *C. glomerata* is no longer extant but the description by Nixon (1974) and reliably identified specimens from Europe and North America (determined by G.E.J. Nixon and W.R.M. Mason respectively) were used for comparative purposes.

C. glomerata may be distinguished from the other two species by the color of the hind femur which is yellow with a small melanic region in the apical 1/6. The hind femora of *C. ayerza* and *C. lesbiae* are uniformly brown. *C. ayerza* and *C. lesbiae* may be distinguished from each other by the dimensions of the medial tergite of the first metasomal segment. That of *C. ayerza* is about as wide as long whereas that of *C. lesbiae* is more than 1.5 times longer

Table 1. Comparison of *Cotesia* species parasitizing *Colias lesbia*.

Characters and states	Taxa
	a = <i>C. ayzerza</i>
	g = <i>C. glomerata</i>
	l = <i>C. lesbiae</i>
1. Hind femur color.	
a) Entirely brown (melanic)	a, l
b) Yellow except for brown in apical 1/6	g
2. Hypopygium of female.	
a) tapering to a sharp point apically	a, l
b) with a deep semicircular emargination apically [c.f. Fig. 46 in Nixon (1974)]	g
3. First metasomal median tergite.	
a) more than 1.5 times longer than wide	g, l
b) about as long as wide	a
4. Sculpture of posteromedial region of mesoscutum, directly anterad mesoscutellar sulcus.	
a) with longitudinal rugosities (Fig. 1)	g
b) lacking longitudinal rugosities (Fig. 2)	a, l

than wide. Other morphological differences between the three species are summarized in Table 1.

There may be a behavioral difference between *C. lesbiae* and the other two species. *C. ayzerza* and *C. glomerata*, like most species of *Cotesia*, are gregarious (Mason

1981, Nixon 1974) with many eggs laid in each host, whereas *C. lesbiae* appears to be a solitary parasitoid (Hamity 1978).

Br  thes did not designate a holotype for *Apanteles ayzerza* and we take this opportunity to designate a lectotype and two paralectotypes. All three specimens are on



Figs. 1–2. Dorsal aspects of mesosomata. 1 (left), *Cotesia glomerata*. The arrow on the mesoscutum indicates longitudinal rugosities; 2 (right), *Cotesia lesbiae*.

the same pin, mounted on one, small, quadrate, piece of paper. The lectotype is a female and is the specimen in the middle of the piece of paper flanked by the two paralectotypes which both appear to be males, but owing to the poor condition of the specimens, sex is difficult to determine. The lectotype is missing both left wings and the right hind wing but it is intact otherwise. All specimens appear to be conspecific. There are four original, hand-written labels on the pin. The uppermost reads "La Pampa 111.1920 J. Williamson". The second reads, "parasite de *Colias lesbia*". The third label is small and has a few marks that are not decipherable; and the fourth reads "Apanteles Ayerza Brèthes". We have also added a red label with the following: "Lectotype Apanteles ayerza Brèthes designated by Sharkey, Finell, and Leathers".

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Seven New Genera of the Subfamily Doryctinae (Hymenoptera: Braconidae) from the Old World

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Abstract.—Seven new genera of the subfamily Doryctinae from the tropical and subtropical regions of the Old World are described and illustrated: *Cryptodoryctes* gen. nov. (type species *Cr. turneri* sp. nov. from South Africa), *Chelonodoryctes* gen. nov. (type species *Ch. inopinatus* sp. nov. from Brunei), *Synspilus* gen. nov. (type species *S. nitidus* sp. nov. from Sarawak), *Bracodoryctes* gen. nov. (type species *B. tergalis* sp. nov. from New Guinea), *Afrospathius* gen. nov. (type species *Af. dispar* sp. nov. from Africa), *Hemispathius* gen. nov. (type species *H. polystenoides* sp. nov. from Uganda), and *Antidoryctes* gen. nov. (type species *An. pronotalis* sp. nov. from Australia). Three further species of *Bracodoryctes* gen. nov. are also described: *B. longitarsus* sp. nov., *B. curvinervis* sp. nov., *B. nigriceps* sp. nov. The affinities of the new genera are discussed.

The Doryctinae are one of the most interesting and diversified subfamilies of Braconidae. More than one hundred and twenty valid genera have been described, which, for the most part, are restricted to tropical and subtropical regions (Shenefelt & Marsh 1976; Belokobylskij 1992; Marsh 1993). The generic richness of the Doryctinae is highest in the Neotropical region but this region has also been the most thoroughly investigated, especially by Paul Marsh, who has described many new genera from there (e.g. Marsh 1993), and has recently provided a key to the genera occurring in the New World (Marsh 1997). In comparison, the generic composition of the Old World fauna is really incomplete but, even so, it would appear that the Old World tropics are home to fewer genera than the New World. This pattern of generic level diversity is, interestingly, the opposite of that found in the closely-related and apparently biologically similar Braconinae which have far more genera in the Old World tropics (Quicke 1987, Quicke 1997).

Phylogenetic relationships between the genera of Doryctinae have until recently been based largely on the relatively impoverished Nearctic and Palaearctic faunas (Fischer 1981, Belokobylskij 1992). Further, the characters used have principally concerned external adult morphology such as the presence and absence of various carinae, sutures, and wing veins, and the shape of the metasoma. The discovery of many new internal characters involving male genitalia (Belokobylskij 1987), the venom apparatus (Quicke *et al.* 1992a) and most recently, the internal sculpture of the ovipositor egg canal (Rahman *et al.* 1998), has greatly increased the possibility of obtaining a meaningful phylogenetic tree. Seven new genera from the Old World tropics and subtropics are described here to make their names available for future publications on the phylogeny of the subfamily (Belokobylskij, Marsh & Quicke in preparation).

Of the new taxa described below, *Chelonodoryctes* gen. nov., whose affinities are

uncertain, is the first doryctine genus in which the 2nd and 3rd metasomal tergites are greatly enlarged, covering the following segments of the metasoma in the same way as is known for various genera of Rogadinae and Lysiterminae. Loss of both the occipital and prepectal carinae is one of the main characteristics of the subfamily Braconinae and is a character used in many older keys for separating the Braconinae from the Doryctinae. The new genus *Bracodoryctes* gen. nov., of which four new species are described below, is the second known doryctine genus without these carinae, the first being *Siragra* Cameron which was correspondingly separated from other doryctines in the tribe Siragrini (Belokobylskij 1994). Transformations of the scape are known in several doryctine genera (e.g. *Syngaster* Brullé, *Pseudodoryctes* Szépligeti, *Siragra* Cameron, *Binarea* Brullé, *Pseudorhopetrocentrus* Granger, *Jarra* Marsh & Austin) as they are among the Braconinae (Quicke 1987). However, the new genus *Synspilus* gen. nov. is the first doryctine in which the scape not only has an apical lobe demarcated by a preapical, transverse carina, but also has a strong basal constriction as in the *Atanycolus* Forster group of genera in the Braconinae (Quicke 1987) which are all parasitoids of bark-boring or subcortical beetles in dead standing or fallen wood. In addition, this genus is included in a group with an apically open 1st subdiscal cell and a strongly reduced vein 2RS (tribe Heterospilini: Belokobylskij 1992). *Cryptodoryctes* gen. nov. is an African genus that appears to be related to *Priosphys* Enderlein and *Odontodoryctes* Granger, with which it shares the following putative synapomorphies: absence of the basoventral tubercle of the hind coxa and the short subbasal cell of the hind wing. It lacks an occipital carina but has a distinct pronope on the anterodorsal part of the neck. Two new genera of the tribe Spathiini are described in this paper. *Afrospathius* gen. nov. is especially interesting because it is

the first genus of the subtribe Psenobolina to be found in the Old World. The male of the type species, *A. dispar* sp. nov., is characterised by the loss of vein r-m of the fore wing (present in the female) and by the presence of a large stigma-like enlargement in the hind wing. *Hemispithius* gen. nov. is related to *Spathiomorpha* Tobias from the Palaearctic and Oriental Regions, and also to the Neotropical genus *Notiospathius* Matthews & Marsh, making it particularly interesting biogeographically.

TERMINOLOGY AND COLLECTIONS

Terminology follows that of Wharton et al. (1997). Because this is inconsistent with the useage by the senior author in many papers on the Doryctinae, a table is provided giving the equivalent new terms as defined by Tobias (1976) (Table 1). The following abbreviations are used: POL—postocellar line, OOL—ocular-ocellar line, Od—maximum diameter of lateral ocellus. Specimens are held in The Natural History Museum, London, England (BMNH), the Bishop Museum, Honolulu (BPBM) and the Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia (ZIP).

DESCRIPTIONS OF NEW TAXA

Cryptodoryctes gen. nov.

Diagnosis.—This new genus is related to two other African genera, *Priosphys* Enderlein and to *Odontodoryctes* Granger. *Cryptodoryctes* differs from the other two by the hind coxa being without dorsal teeth, lack of an occipital carina, the 2nd tergite having lateral depressions, and the presence of a pronope. *Cryptodoryctes* gen. nov. differs from the Neotropical genus *Megaloproctus* Schulz in that the subbasal cell of the hind wing is very short, the occipital carina lost, a pronope is present, and the 2nd metasomal suture has strong lateral breaks.

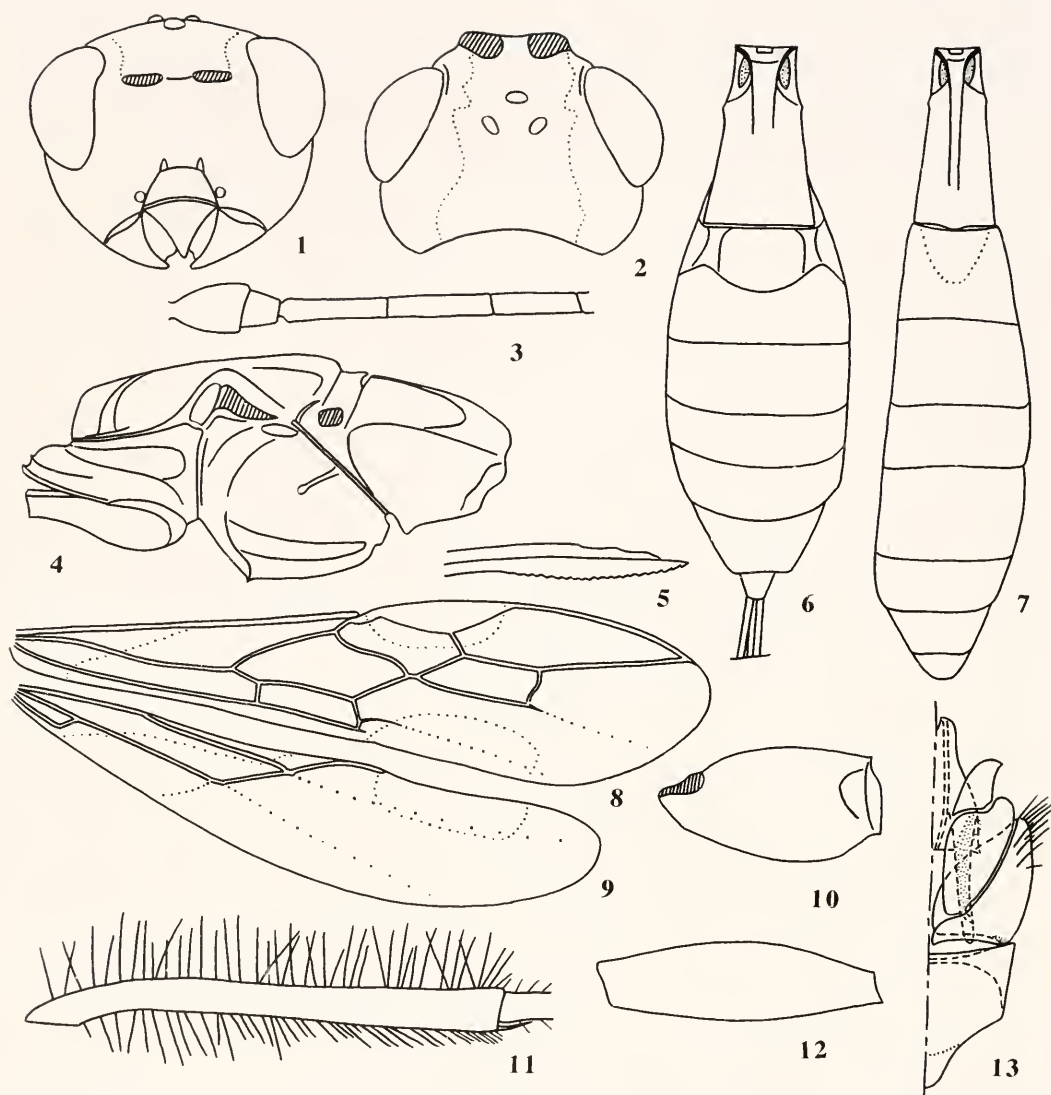
Description.—**Head:** subcubical (Fig. 2), 1.4–1.5 times wider than long medially.

Table 1. Correspondence between wing venation terms employed here (see also Wharton et al. 1997) and those used in many papers on Doryctinae by Belokobylskij following Tobias (1976).

Wharton et al. (1997) and present paper	Tobias (1976)
Forewing cells	
1st subdiscal	brachial
1st discal	discoidal
marginal	radial
2nd submarginal	2nd radiomedial
Forewing veins	
1-1A	anal
1M	basal (lateral)
1M, 2M and 3M	medial (1st-3rd abscissas)
R1a (or R1 if R1b not present)	metacarpus
1cu-a	nervulus
2CUb	parallel
r	1st radial abscissa
3RSa	2nd radial abscissa
3RSb	3rd radial abscissa
2RS	1st radiomedial abscissa
r-m	2nd radiomedial abscissa
1a and 2a	transverse anal veins
m-cu	recurrent
Hind wing cells	
basal	medial
marginal	radial
subbasal	submedial
Hind wing veins	
m-cu	recurrent
C+SC+R and SC+R	costal 1
R1	costal 2
RS	radial
2M (and 3M)	medial
cu-a	nervellus
M+CU	mediocubital 1
1M	mediocubital 2

First flagellar segment nearly as long as 2nd segment. Scapus (Fig. 3) rather short and wide, without apical lobe; almost 1.5 times longer than maximum width. Palpi long; maxillary palpi 6-segmented, labial palpi 4-segmented; 3rd segment of labial palp relatively long. Malar suture absent. Clypeal suture complete. Hypoclypeal depression medium-sized and round (Fig. 1). Face with 2 distinct submedial oval depressions above the clypeal suture. Eyes glabrous. Ocelli in triangle with base 1.2 times longer than sides. Occipital carina entirely absent. Postgenal bridge very nar-

row. Frons not concave and without median keel. **Mesosoma**: depressed. Neck rather long, with convex dorsal lobe; pronope present, but shallow; pronotal keel distinct, near anterior margin of pronotum. Propleural lobe distinct and narrow. Mesonotum not strongly and roundly raised above promesosoma (Fig. 4). Median lobe of mesoscutum without anterolateral angulations (corners). Notauli smooth, deep in anterior half, very shallow on posterior half. Prescutellar depression rather long and sparsely sculptured. Scuto-scutellar suture distinct. Scutellum



Figs. 1-13. *Cryptodoryctes turneri* gen. & sp. nov. 1—head, frontal view; 2—head, dorsal view; 3—basal segments of antenna; 4—mesosoma; 5—apical part of ovipositor; 6—metasoma of female; 7—metasoma of male; 8—fore wing; 9—hind wing; 10—hind coxa; 11—hind tibia; 12—hind femur; 13—male genitalia.

weakly convex, without lateral carinae, striate posteriorly, its length nearly equal to maximum width. Postscutellum without median tooth. Subalar depression shallow and wide. Mesopleural pit deep and round. Sternauli deep, narrow, long, straight and smooth. Prepectal carina distinct and complete. Metapleural flange rather short, wide and pointed apically. Propodeum without margined areas; lat-

eral tubercles and propodeal bridge absent. Propodeal spiracles small and round. *Fore wing*: Pterostigma (Fig. 8) wide; vein r arising from close to middle of pterostigma. Marginal cell slightly shortened. Forewing veins 2RS and r-m present. Vein m-cu antefurcal. Vein 1cu-a postfurcal. First discal cell petiolate. Vein 2CuB arising from posterior quarter of distal side of 1st subdiscal cell. First subdiscal cell closed.

Vein M + CU not curved towards vein 1A. Hind wing (Fig. 9) with 3 hamuli on vein R1. Vein cu-a present. Subbasal cell short. Vein M + CU 0.4 times length of 1M. Vein m-cu present, curved toward base of wing. Basal cell wide; nearly 0.5 times as long as hind wing. Vein RS arising from vein R1. Marginal cell weakly widened apically, without transverse vein. Vein C + SC + R 0.8 times length of SC + R. *Legs*: All tibiae slender. Fore tibia with sparse large spines more or less arranged in a single row. Hind tibia with 1–3 spines on outer side and with area of dense white setae on inner distal edge. Hind coxa rather large, without basoventral tooth (Fig. 10). Femora without anterodorsal protuberances. Hind femur 3.2–3.3 times as long as wide (Fig. 12). Hind tibial spurs rather short and slender, setose, inner spur 0.2–0.25 times as long as hind basitarsus. Hind basitarsus 0.9 times as long as 2nd–5th segments combined. **Metasoma**: First tergite not petiolate, rather wide (Figs. 6, 7). Acrosternite 0.2 times as long as 1st tergite, its apical margin located anterior to spiracles. Dorsople of 1st tergite large; basolateral lobes absent. Spiracular tubercles indistinct, spiracles in basal quarter of 1st tergite; dorsal carinae present on basal half. Second suture fine, with strong breaks laterally. Second tergite with parallel, lateral, wide furrows (Fig. 6). Second to 3rd tergites with separate laterotergites. Hypopygium small, without medioposterior process. Ovipositor longer than metasoma, down-curved apically; apex of dorsal valve with 3 small nodes and apex of ventral valves serrate.

Distribution.—South Africa.

Etymology.—From 'crypticus' (Greek for 'secret') and the generic name *Doryctes*, because this genus is at least superficially similar to the type genus of the subfamily. Gender: masculine.

Type species.—*Cryptodoryctes turneri* sp. nov.

Cryptodoryctes turneri sp. nov.

(Figs. 1–13)

Material examined.—Female HOLOTYPE with the following data: 'S. Africa, R. E. Turner, Brit. Mus. 1923–341', 'Port St. John, Pondoland, June 1–11.1923' (BMNH). Paratypes. 1 female, 'E. Cape Prov., Katberg. 4000 ft, 14–26.XI.1932', 'S. Africa, R. E. Turner, Brit. Mus. 1932–577' (BMNH); 1 female, 'S. Africa, R. E. Turner, Brit. Mus. 1923–547', 'Port St. John, Pondoland, Oct. 1923' (ZIP); 1 male, 'Natal: Kooft. 1500 ft, Sept. 1926', 'S. Africa, R. E. Turner, Brit. Mus. 1926–404' (BMNH).

Description.—Female. **Body length**: 6.8–8.3 mm; fore wing length 6.2–7.0 mm. **Head**: Antennae slender, filiform, 48-segmented. First flagellar segment almost 4.5 times as long as its apical width. Penultimate segment 3.3 times as long as wide, 0.3 times as long as 1st segment, 0.8 times as long as apical segment, which is with short apical spine. Clypeus with very short flange along lower margin. Width of hypoclypeal depression 0.8 times distance from depression to eye. Tentorial pits distinct. Cheek height 0.5 times height of eye, 0.9 times basal width of mandible. Face width 1.2 times eye height and 1.4–1.5 times height of face and clypeus combined. Eye 1.2 times as high as broad. Temple behind eyes roundly narrowed, transverse diameter of eye 1.5 times as long as temple (dorsal view). Frons with shallow longitudinal median furrow. POL 1.1–1.3 times Od, 0.5–0.6 times OOL; Od 0.5 times OOL. Head roundly narrowed below eyes. **Mesosoma**: Length 2.2 times its height. Subalar depression smooth, punctulate on anterior quarter. Propodeum weakly convex and roundly narrowed toward apex. *Wings*: Length of fore wing 3.8–4.0 times its maximum width. Pterostigma 4–5 times as long as wide, 0.9 times as long as vein R1. Vein 3RSa 3.5–3.7 times length of vein r, 0.5 times length of 3RSb, 1.3–1.5 times length of 2RS. Vein 3RSb straight. Second submarginal cell

rather long, not widened apically, its length 2.8 times its width, 1.1 times length of 1st subdiscal cell. First subdiscal cell wide. Distance from vein 1cu-a to vein 1M almost equal to length of 1cu-a. Hind wing 4.6 times as long as wide. *Legs*: Fore tibia with 4–6 spines at one row on inner side and with 5–7 spines on distal margin. Middle tibia without spines on outer side and with 5 spines on distal margin. Hind tarsus as long as hind tibia. Second tarsal segment 0.4–0.5 times as long as 1st segment, 1.4 times as long as 5th segment (excluding pretarsus). Hind basitarsus with narrow lower keel. **Metasoma**: Length of 1st tergite 1.4–1.5 times its apical width; apical width 1.8–2.0 times its basal width. Length of 2nd tergite 0.4–0.5 times its basal width, 1.2–1.3 times length of 3rd tergite. Ovipositor sheath almost 1.1 times as long as metasoma, 0.6 times as long as body, 0.6–0.7 times as long as fore wing. **Sculpture and setosity**: Head smooth; face densely reticulate, smooth medially. Mesoscutum smooth, strongly rugose on great medioposterior area. Scutellum and mesopleura smooth. Pronotum densely rugulose, almost smooth laterally. Metapleura strongly punctulate, with reticulation. Propodeum finely punctulate, with reticulation, partly smooth, with undulate median carina at least on basal third. Legs smooth. First metasomal tergite striate with rugulae, smooth medioposteriorly, remaining tergites smooth. Body with long outstanding pale and sparse setae. Legs with long, outstanding and rather sparse setae, length of setae on dorsal side of hind tibia 1.4–1.8 times as long as maximum width of hind tibia. **Colour**: Head yellowish brown, frons and median part of vertex dark brown. Mesosoma dark reddish brown, promesosoma (except dark dorsal part) and medioposterior spot of mesoscutum yellowish brown. Metasoma light brown, 1st and 7th or 4th–7th tergites dark reddish brown. Antennae almost black. Palpi and tegulae pale yellow. Legs yellow. Wings infusate, with more

or less distinct light spots near pterostigma and along vein 2Cub. Pterostigma pale yellow.

Male. **Body length**: 5.4 mm; fore wing length 5.0 mm. Transverse diameter of eye 1.2 times as long as temple. Antennae slender. First flagellar segment 6 times as long as apical width. Mesosoma narrow, its length 2.4 times its width. Metasoma narrow (Fig. 7). Length of 1st tergite 2.1 times its apical width, apically 1.5 times basal width. Lateral furrow of 2nd tergite shallow. Length of 2nd tergite nearly equal to its basal width. Second suture almost straight. First tergite almost entirely and median area in basal half of 2nd tergite striate. Basolateral areas of propodeum sparse punctulate. Otherwise similar to female.

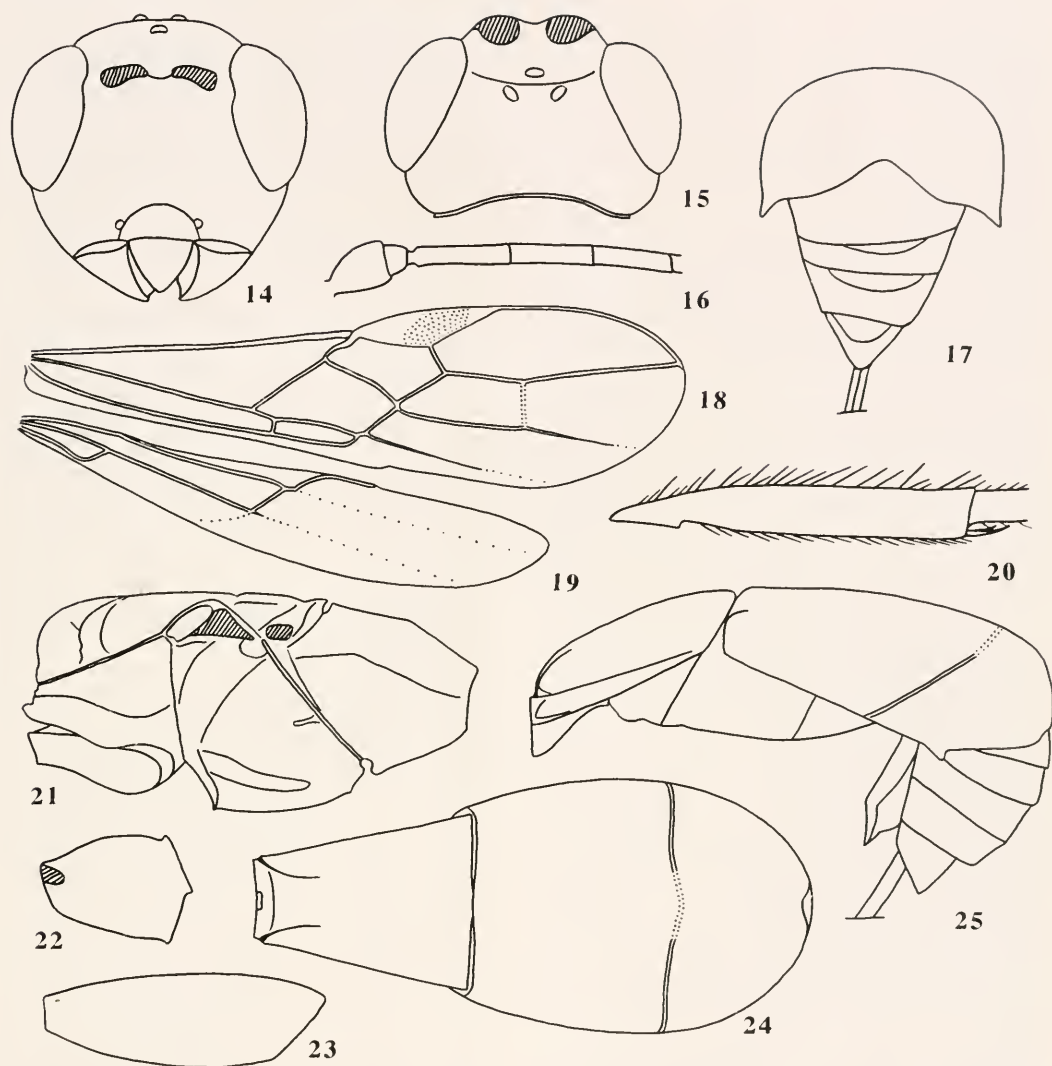
Remarks.—We have studied one female ('S. Africa. R. E. Turner. Brit. Mus. 1924–177', 'Port St. John, Pondoland. 1–17. Mar. 1924'), which is very close to *C. turneri* sp. nov., but differs by having a distinctly shorter 1st metasomal tergite (its length almost equal to apical width). We are not describing a new species for this specimen here because it is possibly only an atypical individual.

Etymology.—In memory of the collector of the type specimen.

Chelonodoryctes gen. nov.

Diagnosis.—This new genus differs from all other Doryctinae in having a carapace formed from the 2nd and 3rd metasomal tergites which conceals all the following segments. The genus is tentatively included in the Doryctini.

Description.—**Head**: weakly transverse (Fig. 15), 1.6 times wider than long medially. Scapus (Fig. 16) wide and short, without apical lobe; 1.3 times longer than maximum width. First flagellar segment simple, slightly longer than 2nd segment. Palpi rather long; maxillary palpi 6-segmented, labial palpi 4-segmented; 3rd segment of labial palp not shortened. Malar suture absent. Hypoclypeal depres-



Figs. 14–25. *Chelonodoryctes inopinatus* gen. & sp. nov. 14—head, frontal view; 15—head, dorsal view; 16—basal segments of antenna; 17—metasoma, posterior view; 18—fore wing; 19—hind wing; 20—hind tibia; 21—mesosoma; 22—hind coxa; 23—hind femur; 24—metasoma, dorsal view; 25—metasoma, lateral view.

sion small and round (Fig. 14). Clypeal suture fine and complete. Frons weakly concave and without median keel. Eyes glabrous. Ocelli in triangle with base 1.3 times side. Occipital carina present dorsally, absent ventrally and therefore not fused with hypostomal carina. Postgenal bridge wide. **Mesosoma:** Neck of promesosoma short, simple dorsally. Pronotal keel fine. Propleural lobe distinct and wide. Mesonotum strongly and roundly

raised above promesosoma (Fig. 21). Notauli deep on anterior half, shallow on posterior half, crenulate. Prescutellar depression long. Scuto-scutellar suture distinct. Scutellum flat, with fine lateral carinae, its length almost equal to maximum width. Postsutellum with short median tooth. Subalar depression shallow and rather wide. Mesopleural pit shallow. Sternauli deep, rather long, straight, widened posteriorly, crenulate. Prepectal ca-

rina distinct and complete. Metapleural flange short, narrow and round apically. Propodeum without marginate areas; lateral tubercles and propodeal bridge absent. Propodeal spiracles small and round. *Fore wing*: Pterostigma (Fig. 18) wide; vein *r* arising from middle of pterostigma. Marginal cell not shortened. Veins 2RS and *m-cu* present. Vein *m-cu* slightly postfurcal. Vein *cu-a* postfurcal. Discoidal cell petiolate. Vein 2CUB interstitial, that is, arising from junction of vein *m-cu* and 1CUB. First subdiscal cell closed. Vein *M + CU* not curved to vein 1A. Hind wing (Fig. 19) with 3 hamuli on vein R1. Vein *cu-a* present. Subbasal cell short. Vein *M + CU* 0.6 times length of 1M. Vein *m-cu* present but unsclerotized and not tubular, curved toward base of wing. Basal cell wide, 0.5 times as long as hind wing. Vein RS arising from vein R1. Marginal cell weakly widened toward apex, without additional transverse vein. Vein *C + SC + R* 0.7 times length of *SC + R*. *Legs*: All tibiae distinctly thickened. Fore and middle tibiae with sparse large spines forming a single longitudinal row. Hind tibia with 6 spines on outer side of apex and with area of dense white setae on inner distal edge. Hind coxa medium sized, with basoventral tooth (Fig. 22). Femora without anterodorsal protuberances. Hind femur 3 times as long as wide (Fig. 23). Hind tibial spurs rather long and slender, almost glabrous, inner spur almost 0.3 times as long as hind basitarsus. Hind basitarsus thickened, 0.55 times as long as 2nd–5th segments combined. **Metasoma**: First tergite not petiolate, wide (Fig. 24). Acrosternite slightly elongate, 0.3 times as long as 1st tergite, its apical margin near level of spiracles (Fig. 25). Dorsople of 1st tergite small, basolateral lobes absent. Spiracular tubercles very small, spiracles placed on basal third of tergite, dorsal carinae present and complete. Second suture present, but shallow and fine. Second tergite without areas (Fig. 24). Second and 3rd tergites enlarged, covering following tergites, with

separate laterotergites. Posterior margin of 3rd tergite with 2 small ventrolateral teeth and distinct semicircular emargination medially (Figs. 17, 25). Hypopygium large, with short pointed process medio-posteriorly. Ovipositor longer than metasoma; apex of dorsal valve with single small nodus, apex of ventral valves serrate.

Distribution.—Island Borneo (Brunei).

Etymology.—From *Chelonus*, a generic name in the subfamily Cheloninae, and *Doryctes* a generic name in the Doryctinae, because of the similar structure of the metasoma to that of chelonines. Gender: masculine.

Type species.—*Chelonodoryctes inopinatus* sp. nov.

***Chelonodoryctes inopinatus* sp. nov.**
(Figs. 14–25)

Material examined.—Female HOLOTYPE with the following data: 'Brunei: Bukit Sulang, nr Lamunin, N. E. Stork' (BMNH).

Description.—Female. **Body length**: 4.1 mm; fore wing length 3.1 mm. **Head**: Antennae with 39 segments. First flagellar segment 4.8 times as long as its apical width. Penultimate segment 4.5 times as long as wide, 0.5 times as long as 1st segment, 0.9 times as long as apical segment. Cheek height 0.5 times height of eye, approximately equal to basal width of mandible. Clypeus without flange along lower margin. Width of hypoclypeal depression 0.7 times distance from depression to eye. Tentorial pits small. Face width nearly equal to eye height and equal to height of face and clypeus combined. Eye 1.2 times as high as broad. Temple behind eyes strongly, roundly narrowed; transverse diameter of eye 2.7 times as long as temple (dorsal view). POL 1.2 times Od, 0.6 times OOL; Od 0.5 times OOL. Head strongly and almost linearly narrowed below eyes. **Mesosoma**: Length twice its height. Pronotum laterally with distinct longitudinal median carina. Subalar depression with coarse longitudinal striae. Propodeum

weakly convex and roundly narrowed toward apex. *Wings*: Length of fore wing 3.5 times its maximum width. Pterostigma 3.8 times as long as wide, 0.7 times as long as vein R1. Vein 3RSa 2.3 times vein r, 0.45 times vein 3RSb, 1.25 times vein 2RS. Second submarginal rather short and wide, its length 2.8 times its width, 1.5 times length of 1st subdiscal cell. First subdiscal cell narrow. Distance from vein cu-a to vein 1M 1.5 times length of cu-a. Hind wing 5.8 times as long as wide. *Legs*: Fore tibia with 5–6 spines at one row on inner side and with 7 spines on distal margin. Middle tibia with 5–6 median spines on outer side and approximately 6 spines on distal margin. Hind tarsus 0.9 times as long as hind tibia. Second tarsal segment 0.5 times as long as 1st segment, nearly as long as 5th segment (without pretarsus). Hind basitarsus with lower keel. **Metasoma**: Length of 1st tergite 1.3 times its apical width; apical width nearly twice its width. Second and 3rd tergites roundly curved at sides. Length of 2nd and 3rd tergites combined 1.6 times basal width of 2nd tergite, 1.3 times its maximum width. Ovipositor sheath 1.8 times as long as metasoma, 0.9 times as long as body, 1.1 times as long as fore wing. **Sculpture and setosity**: Vertex and frons striate, with granulation between striae; face and cheek rugulose-reticulate; temple coriaceous in upper two thirds and almost smooth in lower third. Mesoscutum granulose-reticulate, rugose in large medioposterior area. Scutellum densely granulate. Mesopleura coarsely rugose-reticulate. Propleura rugose. Metapleura and propodeum coarsely and densely reticulate. Hind coxa rugulose dorsally, granulate laterally; hind femur and tibia finely granulate. First and 2nd tergites entirely and basal two thirds of 3rd tergite striate with short transverse rugulae between striae; apical third of 3rd tergite reticulate. Mesosoma with short dense (especially on mesoscutum) white setae. Legs with short, semi-erect, pale, and rather dense setae, length of setae on

dorsal side of hind tibia 0.7–0.9 times as long as maximum width of hind tibia. **Colour**: Mesosoma and 1st–3rd metasomal tergites black with reddish tint. Head reddish brown. Sternites and apical segments of metasoma light brown. Palpi pale yellow. Antennae light reddish brown, darkened toward apex. Tegulae light brown. Legs yellow. Ovipositor sheath black. Wings faintly infusate. Pterostigma yellow, with large brown spot in apical half.

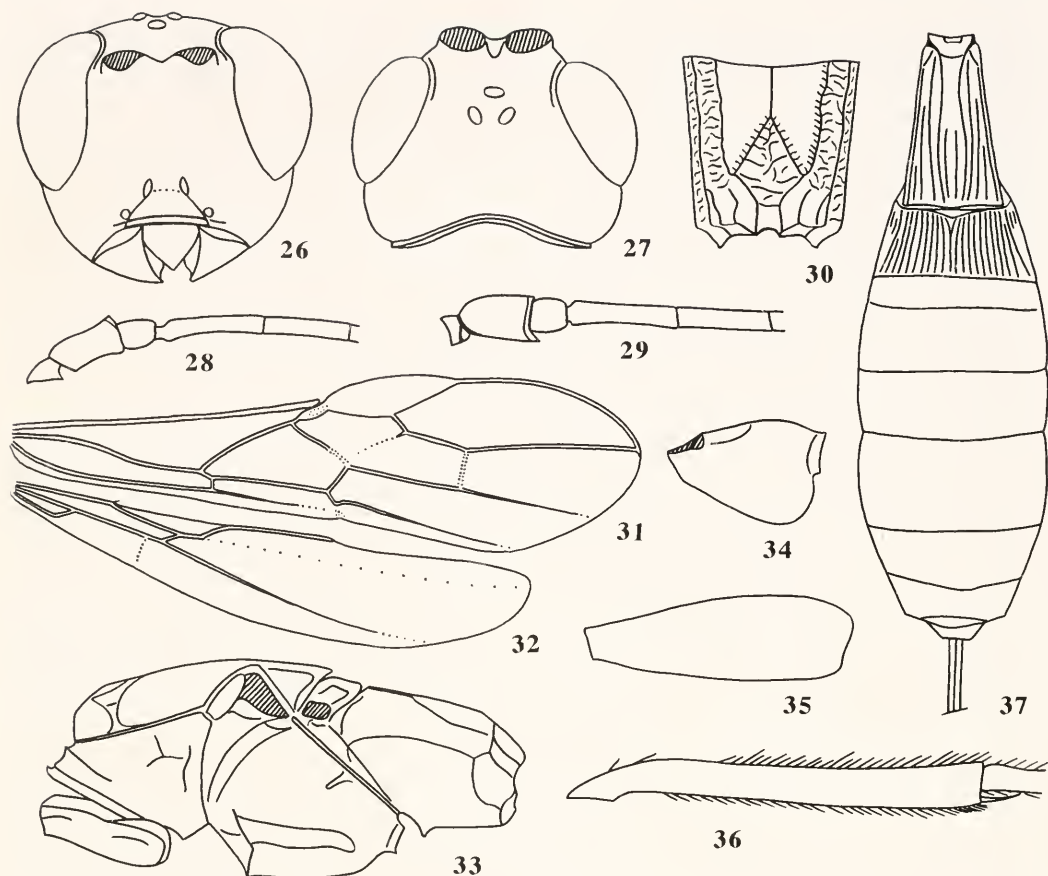
Male unknown.

Etymology.—From Latin '*inopinatus*' meaning 'unexpected' because the construction of the carapace is very unusual for members of the Doryctinae.

Synspilus gen. nov.

Diagnosis.—This new genus appears to be related to *Heterospilus* Haliday from which it differs by the presence of a narrow but distinct apical lobe on the scape and by a constriction at the base of the scape, the presence of distinct lateral carinae on the prepectus, hind coxa without a basoventral tooth, and the clypeus with double lower carinae. *Synspilus* and *Heterospilus* share the following synapomorphies: 1st subdiscal cell open apically, vein 2RS of forewing strongly reduced, basal cell of hind wing narrow, forewing vein m-cu almost perpendicular to vein 2M and propodeum with marginate basolateral areas.

Description.—**Head**: subcubical (Fig. 27), 1.5 times wider than long medially. Scape (Figs. 28, 29) rather short and wide, with strong basal constriction and with small semi-oval apical lobe and preapical keel along inner side; 1.7 times longer than maximum width. First flagellar segment simple, longer than 2nd segment. Palpi rather long; maxillary palpi 6-segmented, labial palpi 4-segmented; 3rd segment of labial palp not shortened. Malar suture very shallow. Hypoclypeal depression rather small and round (Fig. 26). Clypeus with double lower carinae. Clypeal suture



Figs. 26-37. *Synspilus nitidus* gen. & sp. nov. 26—head, frontal view; 27—head, dorsal view; 28—basal segments of antenna, dorsal view; 29—basal segments of antenna, lateral view; 30—areas of propodeum; 31—fore wing; 32—hind wing; 33—mesosoma; 34—hind coxa; 35—hind femur; 36—hind tibia; 37—metasoma.

distinct, shallow dorsally. Face with 2 distinct submedian oval depression above clypeal suture. Eyes glabrous. Frons weakly concave and without median keel, with lateral keels along border of eyes. Ocelli in equilateral triangle. Occipital carina present, complete, fused with hypostomal carina. Postgenal bridge distinct. **Mesosoma:** Neck of promesosoma short, simple dorsally. Pronotal keel distinct, near mesoscutum. Propleural lobe distinct and wide. Mesonotum highly and almost perpendicularly raised above promesosoma (Fig. 33). Median lobe of mesoscutum with short anterolateral angulations (corners). Notauli deep and smooth. Prescutellar depression rather long and smooth, with

sparse striae. Scuto-scutellar suture distinct. Scutellum weakly convex, without lateral carinae, its length 1.3 times maximum width. Postscutellum with short median keel. Subalar depression rather deep and narrow. Mesopleural pit very shallow and elongate. Sternauli deep, rather long, straight, and smooth. Prepectal carina distinct and complete. Prepectus with 2 lateral longitudinal parallel carinae. Metapleural flange rather short, narrow and pointed apically. Propodeum with marginal areas; lateral tubercles and propodeal bridge absent. Propodeal spiracles small and round. *Fore wing:* Pterostigma wide (Fig. 31); Vein r arising almost from middle of pterostigma. Marginal cell not

shortened. Vein 2RS largely unsclerotized, indistinct. postfurcal. Discoidal cell petiolate. Vein 2CUB distinctly curved basally. First subdiscal cell open apically. Vein M + CU not curved towards vein 1A. Hind wing (Fig. 32) with 3 hamuli on vein R1. Vein cu-a present. Subbasal cell short. Vein M + CU 0.7 times length of 1M. Vein m-cu present, antefurcal, almost perpendicular to medial vein, unsclerotized. Basal cell narrow, 0.33 times as long as hind wing. Hindwing vein RS arising from vein R1. Marginal cell weakly narrowed apically, without additional transverse vein. Vein C + SC + R 1.4 times length of SC + R. *Legs*: All tibiae slender. Fore tibia with numerous small and dispersed spines. Hind tibia with 4 spines on outer side and with row of dense white setae on inner distal edge. Hind coxa without basoventral tooth (Fig. 34). Femora without anterodorsal protuberances. Hind femur 3 times as long as wide (Fig. 35). Hind tibial spurs rather short and slender, sparsely setose, inner spur almost 0.25 times as long as hind basitarsus. Hind basitarsus 0.4 times as long as 2nd–5th segments combined. **Metasoma**: First tergite not petiolate, narrow (Fig. 37). Acrosternite 0.25 times as long as 1st tergite, its apical margin distinctly anterior to spiracles. Dorsople of 1st tergite distinct; basolateral lobes absent; spiracular tubercles indistinct, spiracles on basal third of tergite; dorsal carinae present and complete. Second suture distinct, very weakly curved laterally. Second tergite with very small semi-oval mediobasal area. 3rd tergite with transverse fine furrow in basal third. Second to 5th tergites with separate laterotergites. Hypopygium small, with very short and pointed process medioposteriorly. Ovipositor shorter than metasoma.

Distribution.—Sarawak.

Etymology.—From the parts of names of 'Syngaster' and 'Heterospilus' (genera of Doryctinae), because the new genus includes the characters of both these gen-

era, though it is not related to the former. Gender masculine.

Type species.—*Synspilus nitidus* sp. nov.

***Synspilus nitidus* sp. nov.**

(Figs. 26–37)

Material examined.—Female HOLOTYPE with the following data: 'Sarawak: 4th div. Gn. Mulu, RGS Exp., II-III 1978, N.M.Collins' (BMNH).

Description.—Female. **Body length**: 4.6 mm; fore wing length 3.2 mm. **Head**: Antennae slender, remaining 14 segments. First flagellar segment 5.3 times as long as its apical width, 1.1 times as long as 2nd segment. Width of hypoclypeal depression 0.6 times distance from depression to eye. Cheek height 0.3 times height of eye, 0.7 times basal width of mandible. Tentorial pits small. Face width 0.9 times eye height and 0.85 times height of face and clypeus combined. Eye 1.1 times as high as broad. Temple behind eyes strongly roundly narrowed, transverse diameter of eye twice as long as temple (dorsal view). POL 0.6 times Od, 0.3 times OOL; Od 0.4 times OOL. Head strongly and roundly narrowed below eyes. **Mesosoma**: Length 2.3 times its height. Subalar depression smooth, with 4 striae in upper half. Propodeum roundly narrowed toward apex. *Wings*: Pterostigma 3.2 times as long as wide, 0.7 times as long as vein R1. Vein 3RSa 3.3 times vein r, 0.4 times vein 3RSb, nearly equal to vein 2RS. Second submarginal long, its length 3 times maximum width, equal to length of 1st subdiscal cell. First subdiscal cell narrow. Distance from vein cu-a to vein 1M 0.5 times length of cu-a. Hind wing 5.3 times as long as wide. *Legs*: Fore tibia with numerous spines dispersed along inner side and with 5 spines on distal margin. Middle tibia with numerous spines on outer side and 5 spines on distal margin. Hind tarsus 1.1 times as long as hind tibia. Second tarsal segment 0.8 times as long as 1st segment, 1.4 times as long as 5th segment (without pretarsus). Hind basitarsus without lower keel.

Metasoma: Length of 1st tergite 1.8 times its apical width; apical width 1.6 times its basal width. Length of 2nd tergite 0.65 times its basal width, 0.85 times length of 3rd tergite. Ovipositor sheath 0.55 times as long as metasoma, 0.25 times as long as body, 0.4 times as long as fore wing. **Sculpture and setosity:** Vertex and frons smoothly striate, frons smooth medially; face coarsely reticulate; temple smooth. Mesosoma smooth. Propleura smooth, striate on lateral area. Metapleura smooth on anterior half, reticulate on posterior half. Propodeum with large and pentagonal areola, median carina slightly shorter than anterior sides of areola; basolateral areas smooth, rest part of propodeum (including near carinae) rugose. Legs smooth. First and 2nd metasomal tergites striate, rest part of metasoma smooth. Mesonotum glabrous almost entirely. Legs with short, semi-erect, pale, and dense setae, length of setae on dorsal side of hind tibia 0.4–0.8 times as long as maximum width of hind tibia. **Colour:** Body reddish brown, partly lighter. Antennae light brown, slightly darkened toward apex. Palpi pale yellow. Tegulae light brown. Legs light reddish or yellowish brown. Wings faintly infuscate. Pterostigma dark brown.

Male unknown.

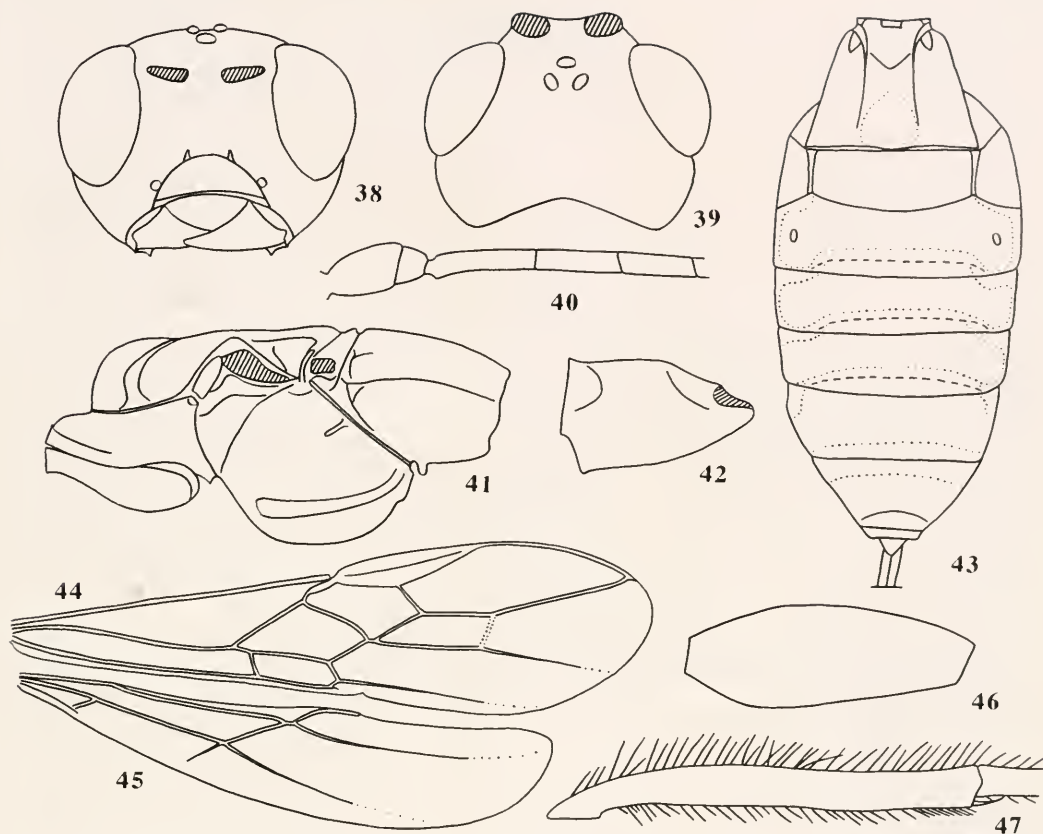
Etymology.—From Latin '*nitidus*' meaning 'shining' because most of the body of this species is without sculpture and is shiny.

Bracodoryctes gen. nov.

Diagnosis.—This new genus differs from all other genera of the tribe Doryctini (to which it might belong) by the absence of both the occipital and prepectal carinae. Both of these carinae are also absent in *Siragra* Cameron of the Siragrini, from which the new genus differs in having a simple scape, i.e. without an apical lobe and additional carina, by having the propodeal bridge indistinct, the hind coxa with a ba-

soventral tooth, and the basal ring of the male genitalia with a dorsal bridge.

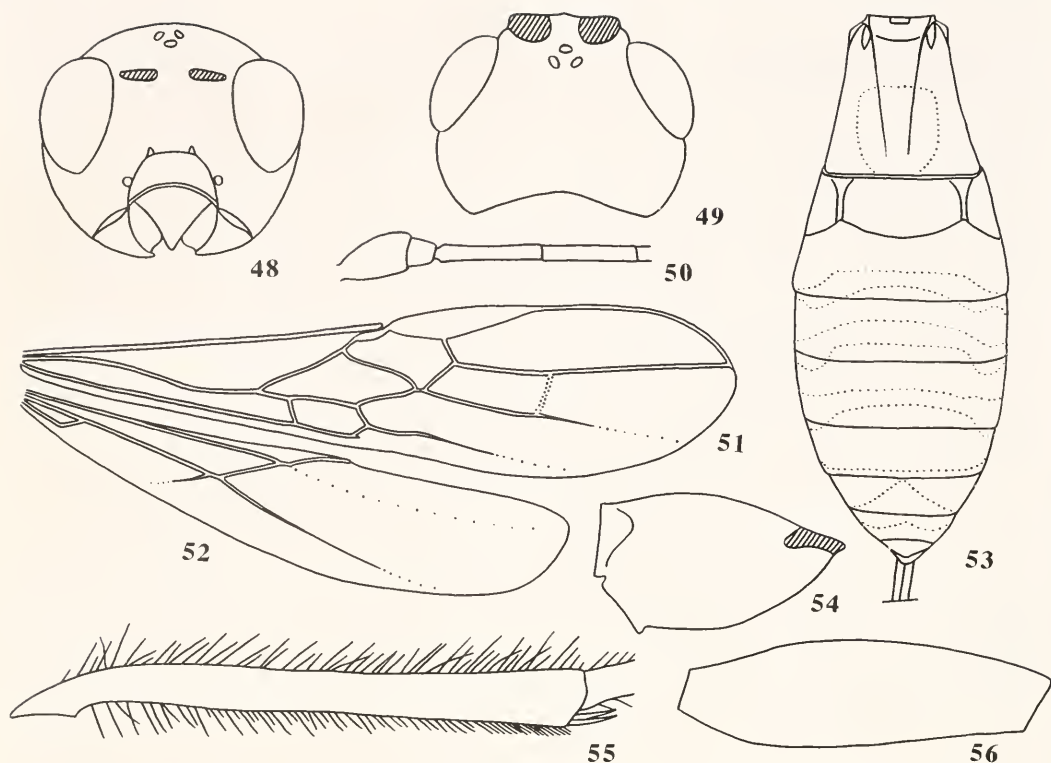
Description.—**Head:** subcubical (Figs. 39, 49, 58, 69), 1.4–1.5 times wider than long medially. Scapus (Figs. 40, 50, 59, 70) rather wide and short, without any lobes; 1.7–2.0 times longer than maximum width. First flagellar segment longer than 2nd segment. Palpi rather long; maxillary palpi 6-segmented, labial palpi 4-segmented; 3rd segment of labial palp long. Malar suture absent. Hypoclypeal depression rather great and round (Figs. 38, 48, 57, 68). Clypeal suture narrow and complete. Face with 2 small, but usually distinct submedian oval depression above clypeal suture. Eyes shortly setose. Frons not concave and without median keel. Ocelli almost in equilateral triangle. Occipital carina absent. Postgenal bridge very narrow. **Mesosoma:** Neck of promesosoma rather long or short, with more or less distinct dorsal lobe. Pronotal keel present. Propleural lobe distinct and wide. Mesonotum rather strongly and roundly raised above promesosoma (Figs. 41, 60, 71). Median lobe of mesoscutum without anterolateral angulations (corners). Notauli usually smooth, deep in anterior half, absent in posterior half, sometimes entirely absent. Prescutellar depression rather long or short, smooth. Scuto-scutellar suture distinct. Scutellum weakly convex, without lateral carinae, its length nearly equal to its maximum width. Postscutellum without median tooth. Subalar depression deep, rather narrow and smooth. Mesopleural pit very shallow and long. Sternauli shallow, long, straight and smooth. Prepectal carina absent. Prepectus simple. Metapleural flange rather long, narrow and pointed apically. Propodeum without marginate areas; lateral tubercles absent; propodeal bridge absent, rarely present, but very narrow. Propodeal spiracles rather small and round or oval. **Fore wing:** Pterostigma (Figs. 44, 51, 63, 74) rather narrow; Vein r arising before middle of pterostigma. Marginal cell not shortened



Figs. 38–47. *Bracodoryctes tergalis* gen. & sp. nov. 38—head, frontal view; 39—head, dorsal view; 40—basal segments of antenna; 41—mesosoma; 42—hind coxa; 43—metasoma; 44—fore wing; 45—hind wing; 46—hind femur; 47—hind tibia.

or only slightly shortened. Veins 2RS and r-m present. Vein m-cu usually antefurcal, rarely postfurcal (Fig. 74). Vein m-cu postfurcal. Discoidal cell petiolate. Vein 2CUB arising from middle or posterior third of apical side of 1st subdiscal cell. First subdiscal cell closed. Vein M + CU not curved to vein 1A. Hind wing (Figs. 45, 52, 64, 75) with 4–5 hamuli on vein R1. Vein cu-a present. Subbasal cell short. Vein M + CU 0.3–0.5 times length of 1M. Vein m-cu present, slightly curved toward base of wing. Basal cell narrow, nearly 0.5 times as long as hind wing. Vein RS arising from vein R1. Marginal cell almost parallel-sided, weakly narrowed near apex, without additional transverse vein. Vein C + SC + R 0.4–0.6 times length of

SC + R. *Legs*: All tibiae slender. Fore and middle tibiae with sparse large spines arranged in single longitudinal row. Hind tibia with 3 spines on outer side and with area of dense white setae on inner distal edge. Hind coxa with distinct basoventral tooth in females (Figs. 42, 54, 61, 76), but not in males (Fig. 77). Femora without anterodorsal protuberances. Hind femur 3.0–3.5 times as long as wide (Figs. 46, 56, 66, 78). Hind tibial spurs entirely or partly setose, rather short and slender, inner spur 0.2–0.3 times as long as hind basitarsus. Hind basitarsus 0.7–0.9 times as long as 2nd–5th segments combined, rarely equal to its. *Metasoma*: First tergite not petiolate, wide (Figs. 43, 53, 62, 72). Acrosternite nearly 0.2 times as long as 1st tergite,



Figs. 48–56. *Bracadoryctes longitarsus* gen. & sp. nov. 48—head, frontal view; 49—head, dorsal view; 50—basal segments of antenna; 51—fore wing; 52—hind wing; 53—metasoma; 54—hind coxa; 55—hind tibia; 56—hind femur.

its apical margin located anterior to spiracles. Dorsople of 1st tergite very large; basolateral lobes absent. Spiracular tubercles indistinct, spiracles placed in basal third of 1st tergite; dorsal carinae present. Second suture present, distinctly curved laterally; sometimes very fine. Second tergite with lateral, shallow, parallel or oblique furrows. Second to 4th tergites with separate laterotergites. Hypopygium

medium-sized, with short or long obtuse process medioposteriorly. Ovipositor longer or shorter than metasoma.

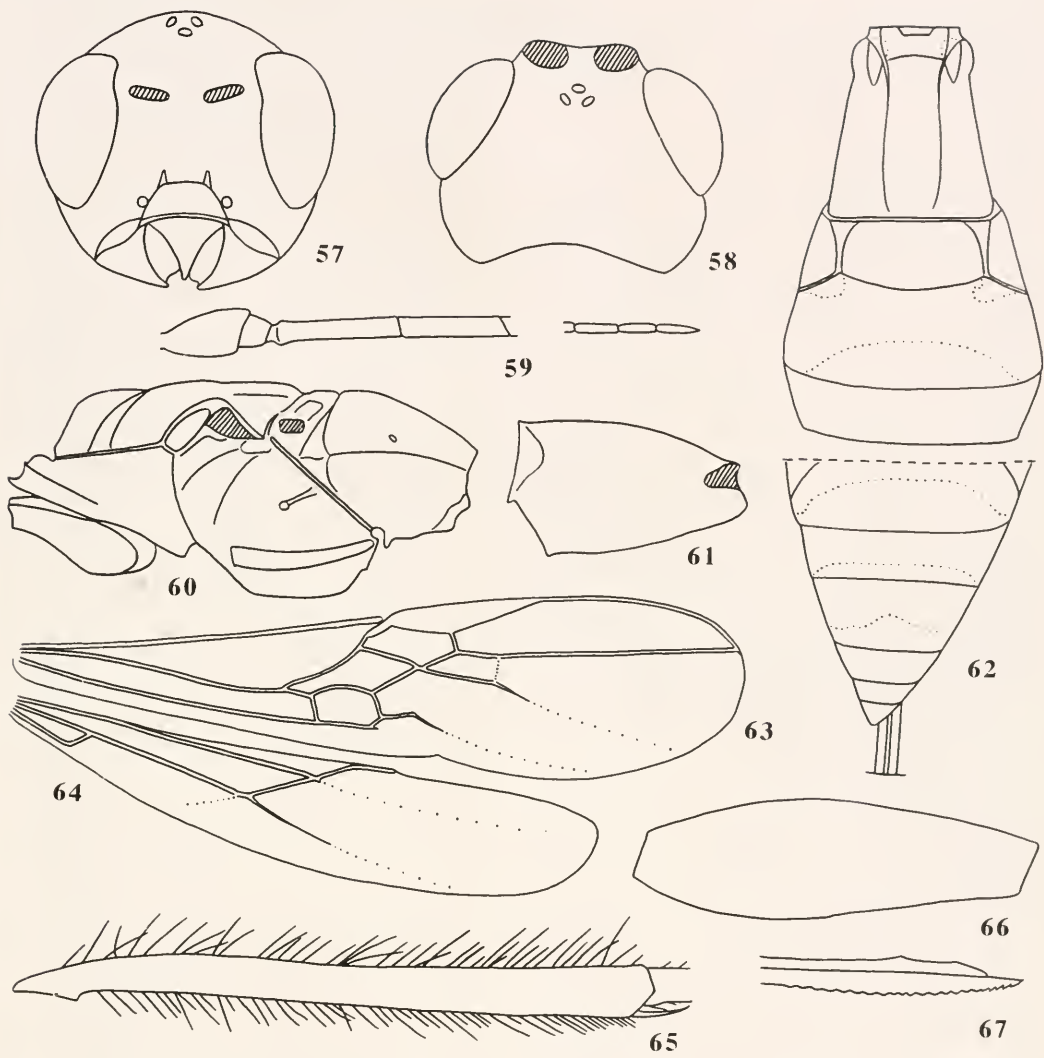
Distribution.—New Guinea.

Etymology.—From 'Bracon' and 'Doryctes' (generic names from the subfamilies Braconinae and Doryctinae), because the new genus displays characters of both these genera. Gender masculine.

Type species.—*Bracadoryctes tergalis* sp. nov.

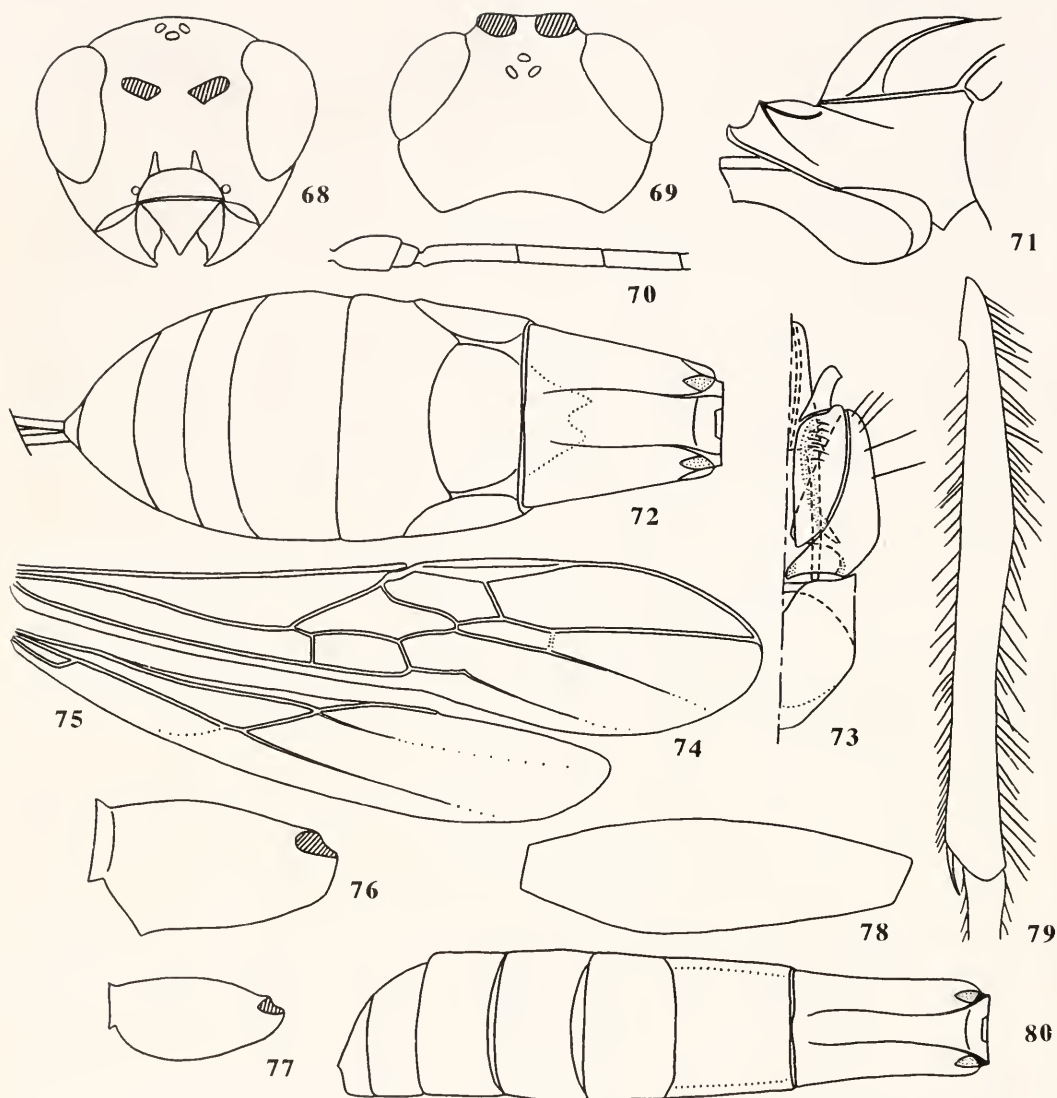
KEY TO SPECIES OF *BRACADORYCTES* gen. nov.

- 1 Face width 0.85 times height of face and clypeus combined. First metasomal tergite short, its length 0.75 times apical width. Ovipositor sheath short, 0.6 times as long as metasoma, 0.4 times as long as fore wing. Legs black. Metapleura entirely sculptured. *B. tergalis* sp. nov.
- Face width 1.1–1.3 times height of face and clypeus combined. First metasomal tergite long, its length nearly equal to apical width. Ovipositor sheath long, 1.1–1.45 times as long as



Figs. 57–67. *Bracadoryctes curvinervis* gen. & sp. nov. 57—head, frontal view; 58—head, dorsal view; 59—basal and apical segments of antenna; 60—mesosoma; 61—hind coxa; 62—metasoma; 63—fore wing; 64—hind wing; 65—hind tibia; 66—hind femur; 67—apical part of ovipositor.

- metasoma, 0.7–0.85 times as long as fore wing. Legs light or yellowish brown. Metapleura in greater part smooth 2
- 2 Vein m-cu postfurcal. Second metasomal tergite of female only striate on basomedial half. Second metasomal suture very fine. Head black. Body length 8.7–10.5 mm *B. nigriceps* sp. nov.
- Vein m-cu antefurcal. Second metasomal tergite of female striate on all the median part. Second suture distinct. Head light or yellowish brown 3
- 3 Notauli entirely absent. Second submarginal cell long and widened toward apex. Vein 2Cub arising from middle of distal margin of 1st subdiscal cell. First subdiscal cell not wider than 2nd submarginal cell. Dorsal part of neck smooth. Body length 8.5 mm *B. longitarsus* sp. nov.
- Notauli distinct in basal half of mesoscutum. Second submarginal short and not widened



Figs. 68–80. *Bracodoryctes nigriceps* gen. & sp. nov. 68—head, frontal view; 69—head, dorsal view; 70—basal segments of antenna; 71—anterior part of mesosoma; 72—metasoma of female; 73—male genitalia; 74—fore wing; 75—hind wing; 76—hind coxa of female; 77—hind coxa of male; 78—hind femur; 79—hind tibia; 80—metasoma of male.

toward apex. Vein 2Cub arising from posterior third of distal margin of 1st subdiscal cell. First subdiscal cell wider than 2nd submarginal cell. Dorsal part of neck sculptured. Body length 10.0 mm *B. curvinervis* sp. nov.

Bracodoryctes tergalis sp. nov.
(Figs. 38–47)

Material examined.—Female HOLOTYPE

with the following data: 'Papua N.G., Bulolo, 2.IX.1981', 'Castanopsis' sp. billet, H.U.Roberts coll., C.I.E.A. 13485' (BMNH).

Description.—Female. **Body length:** 7.5 mm; fore wing length 6.6 mm. **Head:** Antennae rather slender, remaining 30 segments. First flagellar segment 4.5 times as long as its apical width, 1.2 times as long as 2nd segment. Width of hypoclypeal depression 1.2 times distance from depression to eye. Clypeus with very short flange along lower margin. Tentorial pits distinct. Cheek height 0.3 times height of eye, 0.7 times basal width of mandible. Face width 0.8 times eye height and 0.85 times height of face and clypeus combined. Eye 1.1 times as high as broad. Temple behind eyes roundly narrowed, transverse diameter of eye 1.7 times as long as temple (dorsal view). POL 0.5 times Od, 0.3 times OOL; Od 0.5 times OOL. Head roundly narrowed below eyes. **Mesosoma:** Length nearly twice its height. Neck of promesosoma rather long. Pronotal keel distinct, but not high. Notauli distinct in anterior half only. Pre-scutellar depression rather long. Subalar depression entirely smooth. Propodeum regularly roundly narrowed toward apex. **Wings:** Length of fore wing 3.6 times its maximum width. Pterostigma 4.8 times as long as wide, as long as vein R1. Marginal cell slightly shortened. Vein 3RSa twice vein r, 0.5 times the straight vein 3RSb, 1.5 times vein 2RS. Vein m-cu antefurcal. Second submarginal rather long and narrow, not widened apically, its length 3.3 times its width, 1.3 times length of 1st subdiscal cell. First subdiscal cell wide. Distance from vein cu-a to vein 1M 0.7 times length of cu-a. Hind wing 4.6 times as long as wide. **Legs:** Fore tibia with 7 spines at one row on inner side and with 8 spines on distal margin. Middle tibia with 3 spines on outer side and 5–6 spines on distal margin. Hind tarsus 0.9 times as long as hind tibia. Second tarsal segment 0.4 times as long as 1st segment, 1.2 times as long as 5th segment (without pretarsus). Hind basitarsus with lower keel. **Metasoma:** Length of 1st tergite 0.75 times its apical width; apical width 2.2 times its basal

width. Length of 2nd tergite 0.33 times its basal width, 0.9 times length of 3rd tergite. Ovipositor sheath 0.6 times as long as metasoma, 0.3 times as long as body, 0.4 times as long as fore wing. **Sculpture and setosity:** Head and mesosoma smooth. Mesoscutum striate at small medioposterior area. Neck of promesosoma reticulate-rugulose dorsally. Metapleura punctulate-rugulose. Propodeum smooth at large basolateral areas, remaining part densely and strongly punctulate. Legs smooth. First metasomal tergite (except anterior quarter) densely and strongly punctulate; 2nd tergite rugulose-striate, smooth laterally. Remainder of metasoma smooth. Legs with long, erect and rather dense setae, length of setae on dorsal side of hind tibia 0.7–1.0 times as long as maximum width of hind tibia. **Colour:** Head and legs black with reddish tint. Mesosoma red, pronotum anteriorly and propleura darkened. Metasoma black; greater part of 1st tergite (except medioposterior triangle spot), lateral parts of 2nd and anterolateral parts of 3rd–6th tergites yellow; narrow medioposterior bands of 3rd–6th tergites transparent. Antennae black. Palpi dark reddish brown, almost black. Wings faintly infusate. Pterostigma dark brown.

Male unknown.

Etymology.—From Latin “tergum” because the 1st metasomal tergite is very short.

Bracodoryctes longitarsus sp. nov.
(Figs. 48–56)

Material examined.—Female HOLOTYPE with the following data: ‘New Guinea: Neth., Kuttime, West of Swart Val., 1500 m, Nov. 14, 1958’, ‘J.L. Gressitt Collector’ (BMNH).

Description.—Female. **Body length:** 8.5 mm; fore wing length 8.6 mm. **Head:** Antennae weakly setiform, remaining 47 segments. First flagellar segment 5.5 times as long as its apical width, 1.2 times as long as 2nd segment. Cheek height 0.3 times height of eye, 0.6 times basal width of

mandible. Width of hypoclypeal depression 1.25 times distance from depression to eye. Clypeus with flange along lower margin. Tentorial pits distinct. Face width 0.9 times eye height and 1.1 times height of face and clypeus combined. Eye 1.1 times as high as broad. Temple behind eyes roundly narrowed, transverse diameter of eye 1.2 times as long as temple (dorsal view). POL equal to Od, 0.2 times OOL; Od 0.2 times OOL. Head rather strongly and roundly narrowed below eyes. **Mesosoma:** Length nearly twice times its height. Neck of promesosoma long. Pronotal keel distinct and high. Notauli entirely absent. Prescutellar depression short. Subalar depression entirely smooth. Propodeum weakly regularly roundly narrowed toward apex. **Wings:** Length of fore wing 4 times its maximum width. Pterostigma 4.8 times as long as wide, 0.8 times as long as vein R1. Marginal cell not shortened. Vein 3RSa 4 times vein r, 0.6 times the straight vein 3RSb, 2.4 times vein 2RS. Vein m-cu antefurcal. Second submarginal long and wide, distinctly widened toward apex, its length 2.7 times its maximum width, 1.7 times length of 1st subdiscal cell. First subdiscal cell wide. Distance from vein cu-a to vein 1M 1.3 times length of cu-a. Hind wing 4.8 times as long as wide. **Legs:** Fore tibia with 9 spines at almost one row on inner side and with 6 spines on distal margin. Middle tibia with 1–2 spines on outer side and 6 spines on distal margin. Hind tarsus 1.2 times as long as hind tibia. Second tarsal segment 0.4 times as long as 1st segment, twice as long as 5th segment (without pretarsus). Hind basitarsus with lower keel. **Metasoma:** Length of 1st tergite equal to its apical width; apical width almost twice its basal width. Length of 2nd tergite 0.4 times its basal width, 0.9 times length of 3rd tergite. Ovipositor sheath 1.4 times as long as metasoma, 0.7 times as long as body, 0.7 times as long as fore wing. **Sculpture and setosity:** Head and mesosoma smooth. Promesosoma smooth. Me-

tableura smooth, rugose in posterior margin. Propodeum smooth at large basolateral areas, remaining part densely punctulate. Legs smooth. First and 2nd (except its smooth lateral parts) metasomal tergites striate; remaining part of metasoma smooth. Legs with long, almost erect and rather dense setosity; setae on dorsal side of hind tibia almost as long as maximum width of hind tibia. **Colour:** Head, mesosoma and legs light or yellowish brown, with reddish tint partly. Whitish yellow: greater part of 1st tergite (except large round black spot in distal half), lateral parts of 2nd, basal thirds of 3rd–7th tergites. Apical third of 3rd–7th tergites transparent; remaining parts of tergites black or dark reddish brown. Antennae dark reddish brown, lighter basally. Palpi yellow. Tegulae light brown. Wings faintly infusate. Pterostigma brown.

Male unknown.

Etymology.—From Latin '*longus*' for 'long' and '*tarsus*' because all legs are rather long.

***Bracodoryctes curvinervis* sp. nov.**

(Figs. 57–67)

Material examined.—Female HOLOTYPE with the following data: 'New Guinea: Neth., Waris, S. of Hollandia, 450–500 m, VII. 24–31–1959', 'T.C.Maa Collector. Bishop' (BPBM).

Description.—Female. **Body length:** 10.0 mm; fore wing length 8.7 mm. **Head:** Antennae setiform, 62-segmented. Apical segment with slender apical spine. Penultimate segment 4 times as long as wide, 0.3 times as long as 1st segment, 0.9 times as long as apical segment. First flagellar segment 6 times as long as its apical width, 1.2 times as long as 2nd segment. Width of hypoclypeal depression 1.2 times distance from depression to eye. Clypeus with flange along lower margin. Tentorial pits distinct. Cheek height 0.25 times height of eye, 0.5 times basal width of mandible. Face width 0.8 times eye height and 1.1 times height of face and clypeus

combined. Eye 1.3 times as high as broad. Temple behind eyes roundly narrowed, transverse diameter of eye 1.6 times as long as temple (dorsal view). POL 0.7 times Od, 0.2 times OOL; Od 0.3 times OOL. Head strongly and roundly narrowed below eyes. **Mesosoma:** Length 2.2 times its height. Neck of promesosoma long. Pronotal keel distinct, but not high. Notauli rather deep, shallow posteriorly, finely crenulate in anterior half. Prescutellar depression rather long. Subalar depression entirely smooth. Propodeum weakly and regularly roundly narrowed toward apex. **Wings:** Length of fore wing 3.6 times its maximum width. Pterostigma 5 times as long as wide, 0.75 times as long as vein R1. Marginal cell not shortened. Vein 3RSa almost twice vein r, 0.2 times the straight vein 3RSb, 1.5 times vein 2RS. Vein m-cu antefurcal. Second submarginal short and narrow, weakly widened toward apex, its length 2.7 times its maximum width, 1.3 times length of 1st subdiscal cell. First subdiscal cell wide. Distance from vein cu-a to vein 1M 0.75 times length of cu-a. Vein 1M and anterior part of 1st subdiscal cell curved. Hind wing 5 times as long as wide. **Legs:** Fore tibia with 7 thick spines at almost one row on inner side and with 8 spines on lower margin. Middle tibia with 3 spines on outer side and 5 spines on lower margin. Hind tarsus 1.1 times as long as hind tibia. Second tarsal segment 0.4 times as long as 1st segment, 1.6 times as long as 5th segment (without pretarsus). Hind basitarsus with lower keel. **Metasoma:** Length of 1st tergite nearly equal to its apical width; apical width almost twice its basal width. Length of 2nd tergite 0.4 times its basal width, 0.7 times length of 3rd tergite. Ovipositor sheath 1.1 times as long as metasoma, 0.6 times as long as body, 0.7 times as long as fore wing. **Sculpture and setosity:** Head and mesosoma smooth. Mesoscutum with 2 striae in medioposterior third. Promesosoma crenulate in narrow elongate area laterally. Metapleura smooth, punctulate-

rugulose in posterior margin. Propodeum smooth at large basolateral areas, remaining part densely punctulate-rugose; with distinct median and furcal carinae. Legs smooth. First and 2nd (except its smooth lateral parts) metasomal tergites striate; remaining part of metasoma smooth. Legs with long, semi-erect and dense setae, length of setae on dorsal side of hind tibia 0.8–0.9 times as long as maximum width of hind tibia. **Colour:** Head, mesosoma and legs light brown, with reddish tint partly. Yellow: greater part of 1st tergite (except round dark spot in distal half), lateral parts of 2nd, base of 3rd–5th tergites, great part of 6th and entirely 7th tergites. Apical thirds of 3rd–7th tergites transparent; remaining parts of tergites dark reddish brown. Antennae dark reddish brown, 2 basal segments lighter. Palpi yellow. Tegulae light brown. Wings faintly infusate. Pterostigma brown.

Male unknown.

Etymology.—From Latin '*curvus*' for 'curved' and '*nervus*' for 'vein' because of the distinctly curved vein 1M and veins of the 1st subdiscal cell.

***Bracodoryctes nigriceps* sp. nov.**

(Figs. 68–80)

Material examined.—Female HOLOTYPE with the following data: 'Songara Pl., Pongdetta, N.G. Papua, *Theobromococoa* Blute. 20.II – 68, E. Hasson' (BMNH). Paratype. 1 male, 'Dutch New Guinea: Japen Is., Mt. Baduri, 1,000 ft, VIII.1938, L.E. Cheesman, B.M. 1938–593' (BMNH).

Description.—Female. **Body length:** 10.5 mm; fore wing length 9.3 mm. **Head:** Antennae setiform, remaining 58 segments. First flagellar segment 5 times as long as apically wide, 1.2 times as long as 2nd segment. Width of hypoclypeal depression 1.4 times distance from depression to eye. Clypeus with flange along lower margin. Tentorial pits distinct. Cheek height 0.25 times height of eye, 0.55 times basal width of mandible. Face width 0.8 times eye height and 1.2 times height of face and

clypeus combined. Eye 1.2 times as high as broad. Temple behind eyes roundly narrowed, transverse diameter of eye 1.6 times as long as temple (dorsal view). POL 0.6 times Od, 0.3 times OOL; Od 0.45 times OOL. Head rather strongly and almost linearly narrowed below eyes. **Mesosoma:** Length twice its height. Neck of promesosoma rather long. Pronotal keel distinct and high. Notauli deep and smooth in anterior half only, absent in posterior half. Prescutellar depression rather long. Subalar depression entirely smooth. Propodeum weakly regularly roundly narrowed toward apex. **Wings:** Length of fore wing 3.8 times its maximum width. Pterostigma 0.8 times as long as vein R1. Marginal cell not shortened. Vein 3RSa 1.6 times vein r, 0.2 times the straight vein 3RSb, 1.5 times vein 2RS. Vein m-cu postfurcal. Second submarginal rather short and narrow, not widened toward apex, its length 5 times its maximum width, 1.1 times length of 1st subdiscal cell. First subdiscal cell wide. Distance from vein cu-a to vein 1M 0.7 times length of cu-a. Hind wing 5.3 times as long as wide. **Legs:** Fore tibia with 7 thick spines at almost one row on inner side and with 7 spines on distal margin. Middle tibia with 2 spines on outer side and 5 spines on distal margin. Hind tarsus 0.9 times as long as hind tibia. Second tarsal segment 0.4 times as long as 1st segment, 1.5 times as long as 5th segment (without pretarsus). Hind basitarsus with lower keel. **Metasoma:** Length of 1st tergite nearly equal to its apical width; apical width twice its basal width. Length of 2nd tergite 0.5 times its basal width, equal to length of 3rd tergite. Second suture very fine. Ovipositor sheath 1.45 times as long as metasoma, 0.7 times as long as body, 0.85 times as long as fore wing. **Sculpture and setosity:** Head and mesosoma smooth. Promesosoma smooth. Metapleura smooth, punctulate-rugulose in posterior fifth. Propodeum smooth at large basolateral areas, remaining part

reticulate-rugulose. Legs smooth. First metasomal tergite entirely and 2nd in basomedian half striate; remaining part of metasoma smooth. Legs with large long, semi-erect and rather dense setae, length of setae on dorsal side of hind tibia 0.7–0.9 times as long as maximum width of hind tibia. **Colour:** Head black. Mesosoma light reddish brown. Metasoma dark reddish brown, 1st tergite (except medioposterior spot) and sides of 2nd tergite whitish yellow. Antennae reddish brown, 2 basal segments lighter. Palpi yellow. Tegulae light brown. Fore and middle legs light brown, hind leg light reddish brown, yellowish distally. Wings faintly infusate. Pterostigma brown.

Male. Similar to female. Body length 8.7 mm; fore wing length 6.7 mm. Antennae 50-segmented. Penultimate segment 3.7 times as long as wide, 0.8 times as long as apical segment. Mesosoma slender and longer, its length 2.5 times height. Pterostigma 5 times as long as wide. Basoventral tooth of hind coxa indistinct. Metasoma long and narrow. First tergite 1.6 times as long as apical width. Second tergite without lateral furrows, its length approximately equal to basal width, 1.2 times length of 3rd tergite. Second suture rather distinct. Second tergite entirely striate; 3rd tergite striate, basally and apically smooth; 4th and 5th tergites almost entirely finely granulose-striate. Length of setae on dorsal side of hind tibia 1.0–1.2 times as long as maximum width of hind tibia. Genitalia Fig. 73.

Etymology.—From Latin '*nigrum*' for 'black' and '*caput*' for 'head' because the new species has a black head.

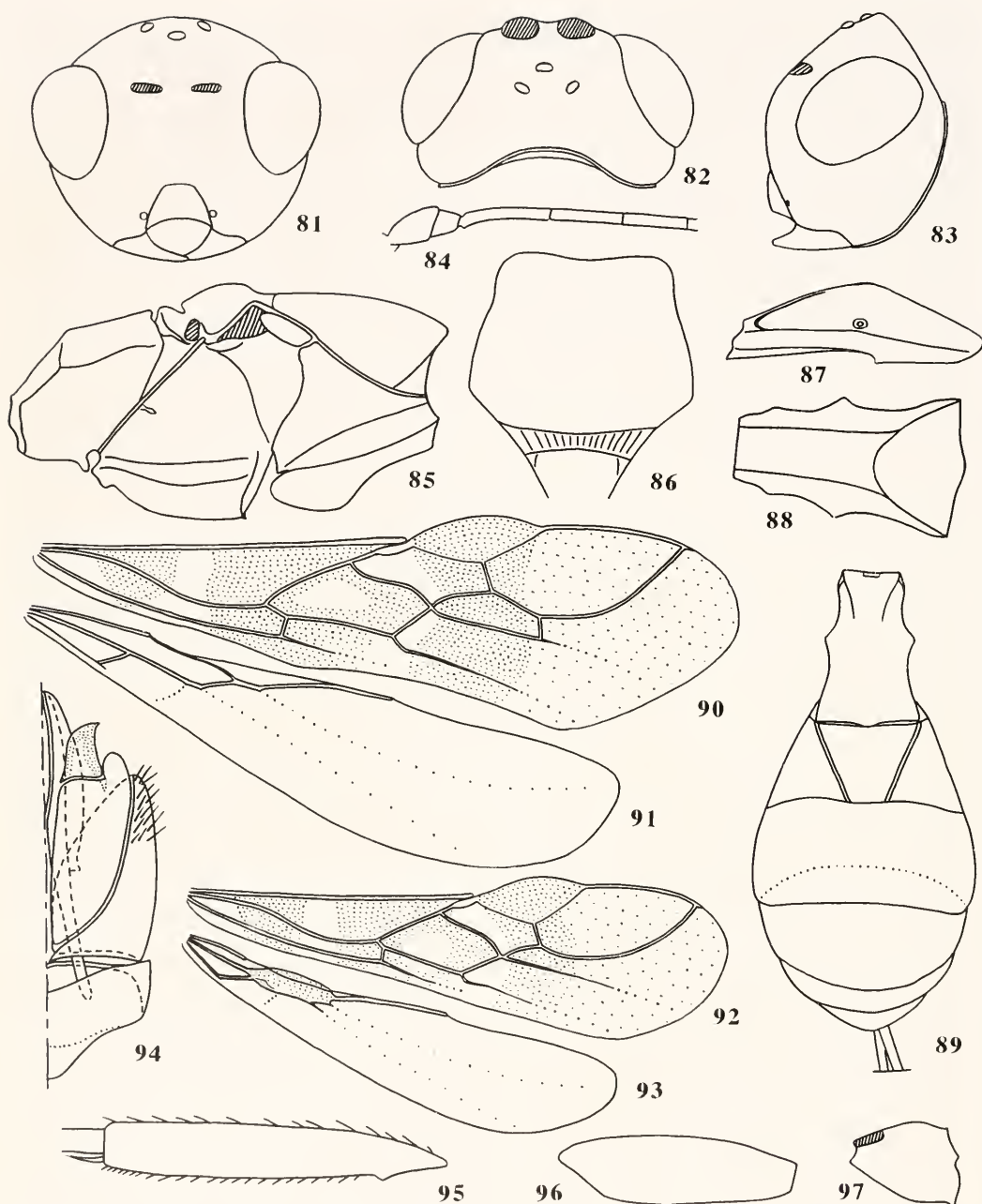
Afrospathius gen. nov.

Diagnosis.—This is the first genus from the subtribe Psenobolina (Spathiini) from Old World. *Afrospathius* gen.n. differs from other psenoboline genera in the absence of notauli, rather short marginal cell, absence of the 2nd radiomedial vein in the male, the male hind wing with stigma-like

enlargement, the 2nd metasomal tergite with a V-shaped figure, and the hind coxa with a basoventral tooth. The occurrence of both a hind wing parastigma in males, and of a basiventral tooth on the hind coxa, in many non-psenoboline doryctines suggests that these are symplesiomorphies and that the new genus is not simply a derived species within that group.

Description.—**Head:** transverse (Fig. 82), nearly 2.0 times wider than long medially. Scapus (Fig. 84) wide and short, without apical lobe; almost 1.5 times longer than maximum width. First flagellar segment simple, slightly curved, 1.1–1.3 times as long as 2nd segment. Palpi rather long; maxillary palpi 6-segmented, labial palpi 4-segmented; 3rd segment of labial palp slightly shortened. Hypoclypeal depression small and round. Clypeus high. Clypeal suture distinct. Malar suture absent (Fig. 81). Face without submedian depressions above clypeal suture. Eyes glabrous. Frons not concave and without median keel. Ocelli in triangle with base 1.3–1.4 times its sides. Vertex distinctly and sharply convex medially. Occipital carina present, absent ventrally and not fused with hypostomal carina. Postgenal bridge very narrow. **Mesosoma:** Neck of promesosoma very short, simple dorsally. Pronotal keel indistinct. Propleural lobe short and narrow. Mesonotum strongly and almost perpendicularly raised above promesosoma, its upper one or two thirds overhanging over promesosoma (Fig. 85); anterior upper border of mesoscutum sharp. Notauli absent or at most very shallow on anterior third. Prescutellar depression rather long and crenulate. Scuto-scutellar suture distinct. Scutellum weakly convex, without lateral carinae, its length almost equal to maximum width. Post-scutellum with small median tooth. Subalar depression rather shallow and wide. Mesopleural pit distinct. Sternauli shallow, long, straight, and crenulate. Prepectal carina distinct and complete. Metapleural flange short, narrow and round

apically. Propodeum without marginate areas; lateral tubercles weak; propodeal bridge absent. Propodeal spiracles small and round. **Fore wing:** Pterostigma (Figs. 90, 92) wide; vein r arising from or slightly before middle of pterostigma. Marginal cell distinctly shortened; vein R1 nearly as long as pterostigma. Veins 2RS and r-m present in female (Fig. 90); in male vein r-m absent (Fig. 92). Vein m-cu interstitial or slightly antefurcal. Vein m-cu postfurcal. Discoidal cell petiolate. Vein 2CUb slightly curved basally. First subdiscal cell open apically. Vein M + CU sigmoid. Hind wing (Figs. 91, 93) with 3 hamuli on vein R1. Vein cu-a present. Subbasal cell medium size. Vein M + CU 1.1–1.4 times length of 1M. Vein m-cu present, curved towards base of wing, unsclerotized. Basal cell narrow, 0.3 times as long as hind wing. Vein RS arising from vein R1. Marginal cell weakly roundly narrowed toward apex, without additional transverse vein. Vein C + SC + R 1.2–1.5 times length of SC + R. Hind wing of male with stigma-like enlargement (Fig. 93). **Legs:** All tibiae distinctly thickened. Fore and middle tibiae with sparse small spines in single longitudinal rows. Hind tibia (Fig. 95) without spines on outer side of apex and with area on dense white setae on inner distal edge. Hind coxa small, with basoventral tooth (Fig. 97). Femora with small anterodorsal protuberances. Hind femur 3.6–3.8 times as long as wide (Fig. 96). Hind tibial spurs rather short and slender, sparsely setose, inner spur almost 0.3 times as long as hind basitarsus. Hind basitarsus 0.6–0.7 times as long as 2nd–5th segments combined. **Metasoma:** First tergite petiolate, but rather wide (Figs. 87, 89). Acrosternite 0.6 times as long as 1st tergite, its apical margin distinctly posterior to spiracles (Fig. 88). Dorsople of 1st tergite very fine; small round basolateral lobes present. Spiracular tubercles distinct and placed in basal third of 1st tergite; dorsal carinae present in basal third only. Second suture distinct, weakly curved lat-



Figs. 81-97. *Afrospathius dispar* gen. & sp. nov. 81—head, frontal view; 82—head, dorsal view; 83—head, lateral view; 84—basal segments of antenna; 85—mesosoma; 86—mesoscutum; 87—First metasomal tergite, lateral view; 88—First metasomal tergite, ventral view; 89—metasoma; 90—fore wing of female; 91—hind wing of female; 92—fore wing of male; 93—hind wing of male; 94—male genitalia; 95—hind tibia; 96—hind femur; 97—hind coxa.

erally. Second tergite with V-like figure (Fig. 89). Second to 6th tergites with separate laterotergites. Hypopygium small, with median pointed process medioposteriorly. Ovipositor longer than metasoma; apex of dorsal valve with 2 very small nodes and apex of ventral valves serrate. Male genitalia (Fig. 94) without volsellar apodema, dorsal bridge and basal lobe of basal ring present.

Distribution.—Africa (Senegal, Cameroun, South Africa).

Etymology.—from 'afro' for Africa, and the doryctine genus *Spathius*, because this genus is related to *Spathius*. Gender masculine.

Type species.—*Afrospathius dispar* sp. nov.

***Afrospathius dispar* sp. nov.**
(Figs. 81–97)

Material examined.—Female HOLOTYPE with the following data: 'Senegal, Bambey, 1944, J. Risbec' (BMNH). Paratypes: 5 females, 11 males, 'Senegal, Bambey, 1944, J. Risbec' (BMNH, ZIP); 2 males, 'Senegal, Bambey, 623, J. Risbec', '13.V.31' (BMNH); 1 female (without fore wings), 'S. Africa, R.E. Turner, Brit. Mus. 1921–476', 'Mossel Bay, Cape Province, 1–14.XI.1921' (BMNH).

Description.—Female. **Body length**: 3.0–4.3 mm; fore wing length 2.2–3.0 mm. **Head**: Antennae 23–24-segmented. First flagellar segment 6.0–6.5 times as long as its apical width. Penultimate segment 4.0–4.5 times as long as wide, 0.5 times as long as 1st segment, nearly as long as apical segment. Apical segment not acuminate. Width of hypoclypeal depression 0.5–0.7 times distance from depression to eye. Clypeus with flange along lower margin. Tentorial pits very small. Cheek height 0.4–0.6 times height of eye, approximately equal to basal width of mandible. Face width 0.9–1.0 times eye height and equal to height of face and clypeus combined. Eye 1.3 times as high as broad. Temple behind eyes weakly roundly narrowed,

transverse diameter of eye 2.5–2.8 times as long as temple (dorsal view). POL 1.5–1.8 times Od, 0.5–0.6 times OOL; Od almost 0.3 times OOL. Head strongly and roundly narrowed below eyes. **Mesosoma**: Length 1.7–1.8 times its height. Mesoscutum weakly and shortly concave medially on anterior sharp margin. Subalar depression widely crenulate, with granulation between crenulae. Propodeum slightly and almost linearly narrowed toward apex, with small discontinuity near middle. **Wings**: Length of fore wing 3.3–3.5 times its maximum width. Pterostigma 2.5–2.8 times as long as wide. Vein 3RSa 1.5–2.0 times vein r, 0.3–0.4 times vein 3RSb, 0.9–1.0 times vein 2RS. Vein 3RSb roundly curved. Second submarginal narrow and rather short, its length 3.3–4.0 times its width, almost equal to length of 1st subdiscal cell. Distance from vein cu-a to vein 1M 0.7–1.0 times length of cu-a. First subdiscal cell rather narrow. Hind wing 4.0–4.7 times as long as wide. **Legs**: Fore tibia with 5–6 spines at one longitudinal row on inner side. Hind tarsus 1.1 times as long as hind tibia. Second tarsal segment 0.5–0.6 times as long as 1st segment, 1.4–1.5 times as long as 5th segment (without pretarsus). **Metasoma**: Length of 1st tergite 1.5–1.7 times its apical width; apical width 1.6–1.8 times its basal width. Length of 2nd tergite 0.7–0.8 times its basal width, 0.7–0.8 times length of 3rd tergite. Ovipositor sheath 1.1–1.4 times as long as metasoma, 0.6–0.7 times as long as body, 0.9–1 times as long as fore wing. **Sculpture and setosity**: Vertex densely striate; frons, face and cheek densely granulate, with sparse rugae; temple striate, with fine granulation. Mesoscutum densely and irregularly reticulate, only granulate in narrow lateral elongate areas. Scutellum granulose-reticulate. Mesopleura coriaceous in lower half, longitudinally striate in upper half. Propleura striate in upper two thirds, granulate in lower third. Metapleura and propodeum rugulose-reticulate. Legs densely and finely granu-

late. First metasomal tergite reticulate, with striations. Second and 3rd tergites striate with fine transverse rugulae between striae. Posterior third of 3rd tergite and 4th–5th tergites entirely very densely granulate. Legs with very short, semi-erect, pale, and sparse setae, length of setae on dorsal side of hind tibia almost 0.3 times as long as maximum width of hind tibia. **Colour:** Mesosoma and metasoma black or dark reddish brown. Head and mesosoma dorsally reddish brown. Palpi dark reddish brown. Antennae light reddish brown, slightly darkened toward apex. Tegulae dark reddish brown. Legs reddish brown, yellowish distally. Ovipositor sheath black, reddish brown basally. Wings hyaline, with several wide dark transverse bands and spots. Pterostigma dark brown. Parastigma and short distal part of vein SC + R pale yellow.

Male: Body length 2.3–4.3 mm; fore wing length 1.7–2.9 mm. Antennae 19–24-segmented. Vein 3RSa regularly roundly curved. Second radiomedial vein absent. Stigma-like enlargement of hind wing narrow, its length nearly equal to or slightly shorter than distance from enlargement to base of wing. Vein SC + R absent. Mesoscutum variable, smooth or sometimes coarsely or finely reticulate. Genitalia Fig. 94. Otherwise similar to female.

Remarks.—We have also examined one male from Cameroun ('Cameroun, Nkoemvon, 23.IX–25.X.1980, D. Jackson'), which represents a second species of this new genus. This specimen differs from *A. dispar* sp. nov. by its more elongate body, its 1st flagellar segment being as long as the 2nd, the first metasomal tergite being narrower and longer, the stigma-like enlargement of the hindwing being smaller, and the sculpture of mesoscutum being finer. We are not describing this species here because we only have a single male specimen.

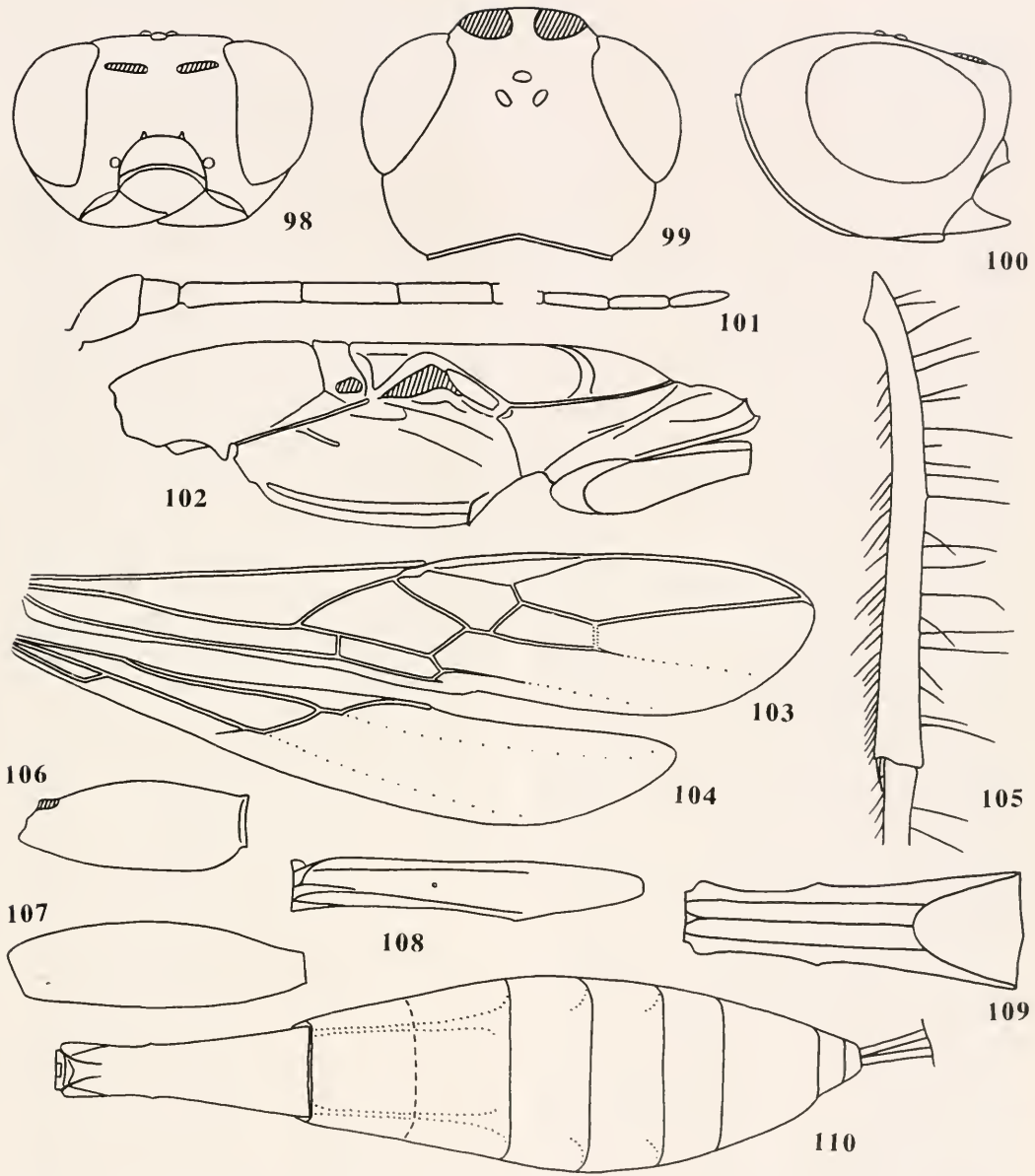
Etymology.—From Latin '*dispar*' meaning 'different' because males and females

are distinctly different in several morphological characters.

Hemispathius gen. nov.

Diagnosis.—This new genus is related to *Spathiomorpha* Tobias and differs by having the hind coxa without basoventral tooth, body strongly depressed, 2nd and 3rd tergites with two lateral parallel shallow furrows, propodeum without marginated areas, and mesoscutum granulate. *Hemispathius* gen. nov. differs from *Notiospathius* Matthew & Marsh by having the 1st subdiscal cell of fore wing closed, body strongly depressed, 2nd and 3rd tergites with two lateral parallel shallow furrows, propodeum without marginated areas.

Description.—**Head:** subcubical (Fig. 99), 1.3 times wider than long medially. Scapus (Fig. 101) wide and rather short, without any lobes; 1.6 times longer than maximum width. First flagellar segment longer than 2nd segment. Palpi rather long; maxillary palpi 6-segmented, labial palp 4-segmented; 3rd segment of labial palpi more or less long. Hypoclypeal depression rather great and oval (Fig. 98). Clypeal suture complete. Malar suture absent. Face with 2 small submedian depressions above clypeal suture. Eyes glabrous. Frons not concave and without median keel. Ocelli in equilateral triangle. Occipital carina present, lower lost and not fused with hypostomal one. Postgenal bridge narrow. **Mesosoma:** Body depressed. Neck of promesosoma long, with distinct convex dorsal lobe. Pronotal keel high, on anterior third of pronotum. Propleural lobe distinct and narrow. Mesonotum very weakly and roundly raised above promesosoma (Fig. 102). Median lobe of mesoscutum without anterolateral angulations (corners). Notauli crenulate, deep in anterior half, absent in posterior half. Prescutellar depression rather short and sculptured. Scuto-scutellar suture distinct. Scutellum flat, without lateral carinae, its maximum width 1.3 times length. Postscutellum with median carina. Subalar depression shal-



Figs. 98–110. *Hemispathius polystenoides* gen. et sp. nov. 98—head, frontal view; 99—head, dorsal view; 100—head, lateral view; 101—basal and apical segments of antenna; 102—mesosoma; 103—fore wing; 104—hind wing; 105—hind tibia; 106—hind coxa; 107—hind femur; 108—First metasomal tergite, lateral view; 109—First metasomal tergite, ventral view; 110—metasoma.

low and rather narrow. Mesopleural pit shallow and long. Sternauli rather deep, long, straight and smooth. Prepectal carina distinct and complete. Metapleural flange rather long, narrow and rounded apically. Propodeum without marginate

areas; lateral tubercles and propodeal bridge absent. Propodeal spiracles small and round. *Fore wing*: Pterostigma (Fig. 103) rather narrow; Vein r arising almost from middle of pterostigma. Marginal cell not shortened. Veins 2RS and r-m present.

Vein m-cu strongly antefurcal. Vein m-cu postfurcal. Discoidal cell petiolate. Vein 2Cub arising from middle of apical side of 1st subdiscal cell. First subdiscal cell closed. Vein M + CU not curved to vein 1A. Hind wing (Fig. 104) with 3 hamuli on vein R1. Vein cu-a present. Subbasal cell short. Vein M + CU 0.6 times length of 1M. Vein m-cu present, curved toward base of wing. Basal cell wide, nearly 0.5 times as long as hind wing. Vein RS arising from vein R1. Marginal cell almost parallel-sided, weakly narrowed near apex, without additional transverse vein. Vein C + SC + R 0.6 times length of SC + R. *Legs*: All tibiae slender. Fore tibia with sparse large spines almost a single row. Hind tibia without spines on outer apical side and with area of dense white setae on inner distal edge. Hind coxa long, without basoventral tooth (Fig. 106). All femora without anterodorsal protuberances. Hind femur 3.2 times as long as wide (Fig. 107). Hind tibial spurs rather short and slender, glabrous or sparsely setose, inner spur almost 0.2 times as long as hind basitarsus. Hind basitarsus 0.8 times as long as 2nd–5th segments combined. **Mesosoma**: First tergite petiolate, narrow (Figs. 108–110). Acrosternite 0.6 times as long as 1st tergite, its apical margin placed posterior to spiracles. Dorsople of 1st tergite small; small round basolateral lobes present. Spiracular tubercles placed in basal third of 1st tergite; dorsal carinae present basally only. Second suture fine and almost straight. Second and 3rd tergites with lateral, shallow, parallel furrows (Fig. 110). Second to 6th metasomal tergites with separate laterotergites. Ovipositor shorter than metasoma; apex of dorsal valve with 2 small nodes and apex of ventral valves serrate.

Distribution.—Africa (Uganda).

Etymology.—From Greek '*hemi*' for 'half' and the doryctine genus name *Spathius*, because this genus has a separate position in the *Spathius*-group. Gender: masculine.

Type species.—*Hemispathius polystenoides* sp. nov.

***Hemispathius polystenoides* sp. nov.**

(Figs. 98–110)

Material examined.—Female HOLOTYPE with the following data: 'Uganda, Kitabwa, 2.12.63, Scolytid, K.W.Brown, B2475' (BMNH).

Description.—Female. **Body length**: 5.4 mm; fore wing length 3.8 mm. **Head**: Antennae slender, weakly setiform, 42-segmented. First flagellar segment 5 times as long as its apical width, 1.3 times as long as 2nd segment. Penultimate segment 5 times as long as wide, 0.5 times as long as 1st segment, as long as apical segment, not acuminate. Width of hypoclypeal depression 1.7 times distance from depression to eye. Clypeus with short flange along lower margin. Tentorial pits distinct. Cheek height 0.2 times height of eye, 0.35 times basal width of mandible. Face width 0.8 times eye height and 1.5 times height of face and clypeus combined. Eye 1.2 times as high as broad. Temple behind eyes roundly narrowed, transverse diameter of eye 1.7 times as long as temple (dorsal view). POL 0.9 times Od, 0.5 times OOL; Od 0.6 times OOL. Head roundly narrowed below eyes. **Mesosoma**: Length 3.4 times its height. Subalar depression entirely smooth. Sternauli deep medially. Propodeum almost linearly narrowed toward apex. *Wings*: Length of fore wing 4.8 times its maximum width. Pterostigma 5.5 times as long as wide, 0.8 times as long as vein R1. Vein 3RSa 4.2 times vein r, 0.35 times the straight vein 3RSb, 1.7 times vein 2RS. Second submarginal rather short, narrowed apically, its length 2.8 times its width, nearly equal to length of 1st subdiscal cell. First subdiscal cell rather narrow. Second abscissa of medial vein long, 0.6 times Vein m-cu. Distance from vein cu-a to vein 1M almost twice length of cu-a. Hind wing 5.8 times as long as wide. *Legs*: Fore tibia with 8 spines at one row on inner side and with 6 spines on lower

margin. Middle tibia with 3 spines on outer side and 4–5 spines on lower margin. Hind tarsus as long as hind tibia. Second tarsal segment 0.4 times as long as 1st segment, 1.4 times as long as 5th segment (without pretarsus). Hind basitarsus with lower keel. **Metasoma:** Length of 1st tergite 3 times its apical width; apical width nearly twice its basal width. Length of 2nd tergite almost equal to its basal width, equal to length of 3rd tergite. Ovipositor sheath 0.6 times as long as metasoma, 0.3 times as long as body, 0.5 times as long as fore wing. **Sculpture and setosity:** Head smooth, face striate. Mesoscutum finely granulate, rugose on greater medioposterior area. Scutellum very finely granulate. Mesopleura smooth. Lateral part of pronotum rugulose. Metapleura rugulose-striate. Propodeum densely punctulate-rugulose. Hind coxa and femur very finely granulate, hind tibia striate. First–3rd metasomal tergites densely rugulose; 4th–6th tergites finely rugulose-reticulate in basal halves; 7th tergite finely coriaceous. Body with long outstanding and rather sparse setae. Legs with long, erect and rather dense setae, length of setae on dorsal side of hind tibia 1.7–2.3 times as long as maximum width of hind tibia, significantly longer than length of setae on ventral side. **Colour:** Head light reddish brown. Mesosoma light reddish brown, dark dorsally. Metasoma dark reddish brown, with light areas laterally and posteriorly on 2nd–6th tergites. Antennae light brown, darkened toward apex. Palpi yellow. Legs yellowish brown; hind femur in subapical two fifths dark. Tegulae yellow. Wings faintly infusate. Pterostigma pale yellow, with brown large median spot.

Male unknown.

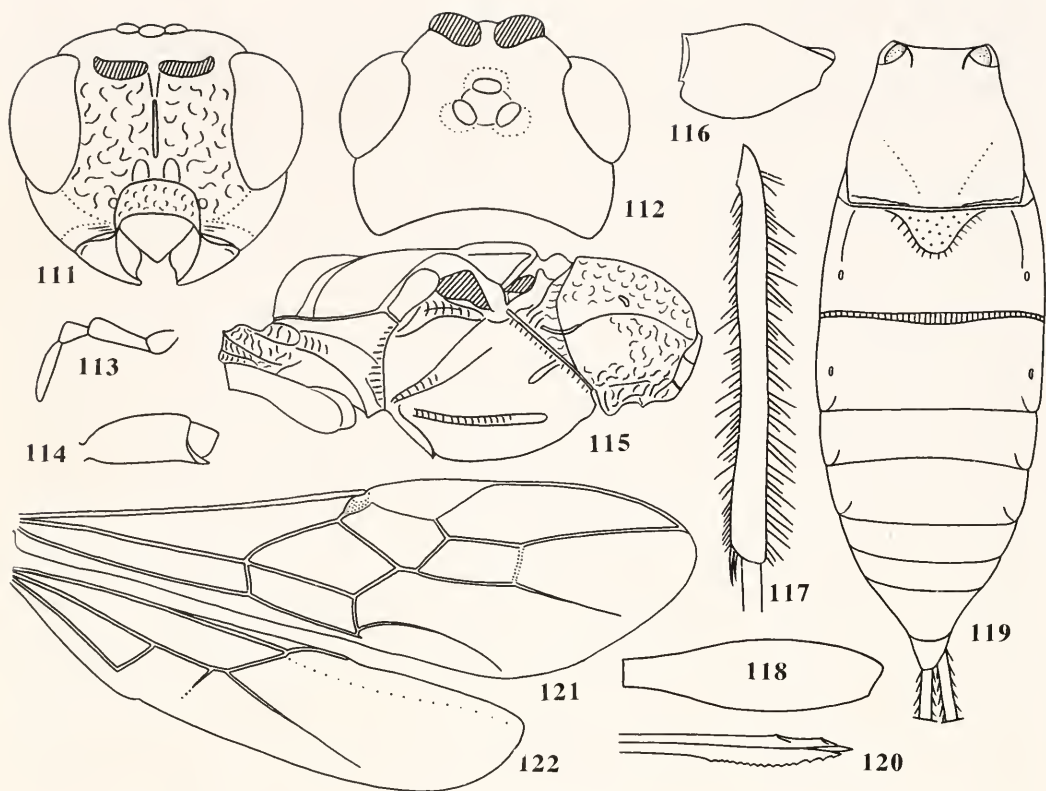
Etymology.—From the generic name *Polystenus* because the habitus is similar to that of *Polystenus* species.

Antidoryctes gen. nov.

Diagnosis.—This new genus belongs to the Binariini (sensu Belokobylskij, 1992)

being most closely related to the Neotropical genus *Liobracon* Szépligeti. The Binariini are defined by the following synapomorphies: occipital carina absent, neck of pronotum with one or two obtuse or pointed tubercles or spines, hind coxa without ventral tubercle, second metasomal tergite with furrows defining an area and usually with the third segment of the labial palp distinctly shortened. All of these are also displayed by the new genus. The new genus differs from *Liobracon* in the scapus not being depressed and lacking the dense apical row of setae, though the scapus does have a distinct apical lobe as in *Liobracon*. It also differs in that the marginal cell of the hind wing lacks an additional transverse vein, and in that the dorsal part of the pronotum is flat and has low lateral tubercles. The new genus also appears to be related to the Australian binariine genus *Acanthodoryctes* Turner from which it differs in having the third segment of labial palp short, frons rather flat, scapus with distinct apical lobe, marginal cell of fore wing not shortened, hind wing with vein m-cu, pronotum without a pair of spine-like protuberances, and 1st metasomal tergite without especially modified setosity (Quicke 1984; Quicke *et al.* 1992b; Austin *et al.* 1994).

Description.—**Head:** subcubical (Fig. 112), 1.3 times wider than medially long. Scapus with distinct semicircular apical lobe (Fig. 114), rather narrow and long, 2.5 times longer than maximum width. Palpi relatively long; maxillary palp 6-segmented, labial palp 4-segmented. Third segment of labial palp shortened, subtriangular, 0.55–0.6 times as long as 2nd and 4th segments separately. Hypoclypeal depression small and round (Fig. 111). Clypeal suture wide and complete. Subocular (malar) suture very shallow. Face with two distinct submedian, oval depressions above clypeal suture. Eyes glabrous. Frons not concave and without a midlongitudinal keel. Ocellar triangle with base 1.2 times longer than sides. Postgenal bridge



Figs. 111–122. *Antidoryctes pronotalis* gen. et sp. nov. 111—head, frontal view; 112—head, dorsal view; 113—labial palp; 114—scapus and pedicellus; 115—mesosoma, lateral view; 116—hind coxa; 117—hind tibia; 118—hind femur; 119—metasoma, dorsal view; 120—apex of ovipositor; 121—fore wing; 122—hind wing.

very narrow. **Mesosoma:** Neck of promesosoma rather long, more or less flat dorsally, with two distinct elongate, obtuse, wide lateral protuberances. Pronotal keel high, concave medially, situated near anterior margin of pronotum. Propleurae without protuberances. Propleural lower lobe distinct and wide. Mesonotum rather highly and roundly raised above promesosoma (Fig. 115). Medial lobe of mesonotum without antero-lateral angulations (corners). Notauli smooth, deep along anterior half, shallow or almost absent posteriorly. Prescutellar depression rather short and sculptured. Scuto-scutellar suture distinct. Scutellum weakly convex, without lateral carinae, 1.3 times longer than maximum width. Postscutellum (median area of metanotum) with short, flat medial tooth. Subalar depression deep,

narrow and placed rather low (Fig. 115). Mesopleural pit shallow. Sternauli deep, long, straight, and crenulate. Prepectal carina distinct and complete, not higher than sternauli. Prepectus with distinct and oblique lateral furrows. Metapleural flange rather long, wide and round apically. Metapleural suture present. Propodeum without areas; lateral, tubercles and propodeal bridge absent. Propodeal spiracles small. **Wings:** Pterostigma of fore wing (Fig. 121) wide; Vein *r* arising almost from middle of pterostigma. Marginal cell slightly shortened. Veins 2RS and *r-m* present. Vein *m-cu* antefurcal. Vein *m-cu* interstitial. Discoidal cell short, petiolate. Vein 2CUB arising from posterior fifth of apical side of 1st subdiscal cell. First subdiscal cell closed. Veins 1a and 2a absent. Hind wing (Fig. 122) with four hamuli on

vein R1. Vein cu-a present. Subbasal cell large. Vein M + CU nearly twice length of 1M. Vein m-cu present, antefurcal, almost perpendicular to medial vein. Basal cell wide, 0.55 times as long as hind wing. Vein RS arising from vein 1M near vein R1. Marginal cell weakly narrowed towards apex, without additional transverse vein. Vein C + SC + R 1.5 times length of SC + R. *Legs*: Fore and middle tibiae with one longitudinal row of widely-spaced, large spines. Hind tibia with two small spines apico-laterally, and with area of dense white setae near apex medially. Hind coxa small, without basoventral tooth (Fig. 116). Femora simple, without dorsal protuberances. Hind femur 3.5 times longer than wide (Fig. 118). Hind tibial spurs rather short, weakly thickened, sparsely setose, inner spur approximately 0.33 times as long as hind basitarsus (Fig. 117). Hind basitarsus 0.7 times length of segments 2–5 combined. **Metasoma**: First tergite not petiolate, wide (Fig. 119), with small round basolateral lobes. Dorsople large. Spiracular tubercles indistinct, spiracles located on basal third of tergite. Acrosternite approximately 0.25 times as long as 1st tergite, its apical margin distinctly before spiracles. Second tergite, with small, semi-oval mediobasal area (Fig. 119). Second suture distinct, weakly curved laterally. Second and third tergites with separate laterotergites. Hypopygium small, with two pointed and separate processes medioposteriorly. Ovipositor longer than metasoma; apex of dorsal valve with 2 small nodes (Fig. 120).

Distribution.—Australia.

Type species.—*Antidoryctes pronotalis* sp. nov.

Etymology.—From Latin “anti” for “contrary” and the generic name *Doryctes*. Gender masculine.

***Antidoryctes pronotalis* sp. nov.**
(Figs. 111–122)

Material examined.—Female HOLOTYPE with the following data: “Millstream Falls,

near Ravenshoe, NQL, 5 Jan. 1967”, “M. V. Lamp, D. K. McAlpine & G. Holloway” (BMNH).

Description.—Female. **Body length**: 15 mm; fore wing length 10.8 mm. **Head**: strongly and roundly narrowed below eyes. Width of hypoclypeal depression 0.8 times distance from depression to eye. Clypeus without carina separating off hypoclypeus. Tentorial pits distinct. Cheek height 0.4 times height of eye, 0.8 times basal width of mandible. Width of face nearly equal to height of eye and equal to combined height of face and clypeus. Eye 1.2 times higher than broad. Temple behind eyes roundly narrowed, transverse diameter of eye 1.5 times length of temple (in dorsal view). POL 0.7 times Od, 0.5 times OOL; Od 0.7 times OOL. **Mesosoma**: 2.2 times longer than high. Subalar depression smooth, crenulate on anterior third. Propodeum convex and roundly narrowed towards apex. *Wing*: Length of fore wing 3.5 times its maximum width. Pterostigma 3.3 times as long as wide, 0.6 times length of vein R1. Parastigma thickened. Vein r arising from middle of pterostigma. Vein 3RSa 3.3 times vein r, 0.4 times the straight vein 3RSb, 1.4 times 2nd radiomedial vein. Second submarginal rather short, twice as long as wide, 0.8 times length of 1st subdiscal cell. First subdiscal cell wide. Vein 2M rather short, 0.3 times length of vein m-cu. Hind wing 4.5 times as long as wide. *Legs*: Fore tibia with longitudinal row of 5–6 spines and with 7 spines on distal margin. Middle tibia with two medial spines and with 6 spines on distal margin. Hind tarsus 0.7 times length of hind tibia. Hind basitarsus 2.0 times longer than 2nd segment. Second segment approximately as long as telotarsus (excluding pretarsus). Hind basitarsus without ventral keel. **Metasoma**: Length of 1st tergite 0.9 times its apical width. Second tergite 0.6 times as long as basally wide, 1.2 times length of 3rd tergite. Ovipositor sheath 1.2 times metasomal length, 0.6 times body length, 1.1 times fore wing

length. **Sculpture and setosity:** Head smooth; face coarsely and irregularly reticulate-rugose. Mesosoma largely smooth; propleura rugose on anterior third, metapleura reticulate rugose, almost smooth on upper, anterior third. Propodeum finely reticulate. Legs smooth. Metasoma smooth, furrow around basal area of 2nd tergite distinctly, sparsely crenulate. Metapleura and propodeum with sparse, long, pale setae. Legs with long, erect, pale, rather sparsely distributed setae; lengths of setae arising from dorsal surface of leg 1.1–1.3 times maximum width of hind tibia. **Colour:** Head yellowish white. Pro- and mesothorax (except posterior side of mesoscutum and scutellum) and 3rd–6th metasomal tergites black. Rest of mesosoma and posterior of metasoma light reddish brown. Metasomal tergites 1 and 2 yellow. Scapus dark reddish brown, pedicel light reddish brown. Palpi yellow. Legs light reddish brown. Fore coxae largely, mid and hind coxae entirely, mid and hind trochanters and hind femur dark reddish brown to black. Mid- and hind tarsi reddish. Tegulae reddish brown. Wings infusate with yellowish tint. Pterostigma and veins on basal quarter yellow, remaining venation dark but becoming paler again towards apex.

Male unknown.

Etymology.—Because the pronotum is likely to show species level differences as in other genera of Binariini.

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Morphometric Analysis and Descriptions of Selected Species in the *Encarsia strenua* Group (Hymenoptera: Aphelinidae)

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Abstract.—The *Encarsia strenua* group is defined using three synapomorphies: presence of 1–3 specialized setae at the apex of the costal cell, a bare area above the stigmal vein and closely placed scutellar sensillae. Few morphological characters were found that could accurately distinguish some species of the *strenua* group because of variability within species and the lack of diagnostic differences among species. The morphometric relationships of females of five closely related species of the *strenua* group were explored using bivariate and multivariate statistical methods. Univariate or bivariate measures could not distinguish all groups, however, all five species were discriminated along the first two canonical variates. Host relationships, although having a strong effect on general size, do not affect the discrimination of taxa. An identification key is provided for six species of the *strenua* group. *Encarsia citri*, *E. protransvena* and *E. strenua* are redescribed. Two new species, *E. bimaculata* and *E. neocala*, are described. *Encarsia sophia* (Girault & Dodd) is proposed as a senior synonym of *E. transvena* (Timberlake).

The genus *Encarsia* (Hymenoptera: Aphelinidae, Coccophaginae) is a diverse and cosmopolitan group of species usually parasitic on Aleyrodidae (whiteflies), Diaspididae (armored scales), or themselves (as autoparasitoids) (Polaszek 1991). A few species are parasitoids of the eggs of Lepidoptera (Polaszek 1991). At present there are more than 200 described species of *Encarsia* (Polaszek *et al.* 1992), and new species are continually being described or recognized. The genus *Encarsia* represents one of the most important parasitic groups used in biological control, and various species are currently being collected as part of intensive foreign exploration efforts to search for parasites of whiteflies of the genus *Bemisia*. Several species of *Encarsia* have demonstrated their importance for control of San Jose Scale (*E. perniciosi* (Tower)) (Clausen 1978), Greenhouse whitefly (*E. formosa* Gahan) (Clausen 1978), Ash whitefly (*E. inaron* (Walker)) (Bellows *et al.* 1992), and Spiny blackfly (*E. smithi* (Silvestri)) (Ku-

wana 1934). New programs are focusing on the control of *Bemisia* with *E. protransvena* Viggiani and *E. sophia* (Girault) and on citrus whitefly in California with *E. variegata* Howard (T. Bellows, pers. comm.). Biological and taxonomic characteristics remain poorly known even for common species of *Encarsia*.

Within *Encarsia*, approximately 29 species groups are recognized by various authors (Viggiani & Mazzone 1979; Hayat 1989; Polaszek *et al.* 1992), with as few as 16 groups in the most recent treatment by Hayat (1998). Few of these groups are recognized by morphological characters and different species may be included in each by various authors. We have rediagnosed the *strenua* species group, which is here recognized by having closely spaced scutellar sensilla (Figs. 5, 20), a group of one to three marginal setae at the apex of the costal cell of the fore wing (Fig. 10, arrow), and a bare area just anterior to the stigmal vein (Fig. 10). The *strenua* group now includes 40 species, more than a third of these previously undescribed.

In this paper we attempt to address problems in the taxonomy of a subset of species, which rank among the more important members of the *strenua* group for the control of economically important whiteflies. Resolution of this complex is necessary before going ahead with an identification key to the 40 recognized species. Morphometric analysis, descriptions and an identification key are presented to express the differences between *E. bimaculata* new species, *E. citri* Ishii (revised status), *E. neocala* new species, *E. protransvena*, and *E. strenua*. One of the most commonly encountered species in agricultural settings, *E. sophia*, can be readily distinguished by discrete morphological attributes from other species in the *strenua* groups, and was not included in the morphometric analyses.

MATERIALS AND METHODS

Morphometric analysis.—In total, 196 females of five species of *Encarsia*, *E. bimaculata* ($n = 61$), *E. citri* (12), *E. neocala* (15), *E. protransvena* (83) and *E. strenua* (24) were measured. Males are rare or unknown for some species and were not included. Measurements were taken from slide-mounted material (Table 1) amassed from collections at the National Museum of Natural History (USNM), University of California (UCRC), Texas A&M University (TAMU), and Instituto di Entomologia F. Silvestri, Portici, Italy (IEUN). *Encarsia protransvena* were included from multiple locations in various Gulf Coast States (Mississippi, Florida, Georgia), Puerto Rico, Colombia, Spain and the Grand Caymans, and several different host whiteflies: *Bemisia tabaci* (Gennadius), *Dialeurodes citri* (Ashmead), *D. citrifolii* (Morgan), *D. kirkaldii* (Kotinsky), *Parabemisia myricae* (Kuwana), and *Trialeurodes abutiloneus* (Haldeman). *Encarsia neocala* were measured from a single collection from New Caledonia reared from *Orchamoplatus* [probably *caledonicus* (Dumbleton)] (Aleyrodidae). *Encarsia citri* were measured

from a single collection in Japan from *D. citri*. *Encarsia bimaculata* were sampled from the Oriental Region (Hong Kong, India, Philippines, Thailand) and the Nearctic Region (Florida, Texas) and reared only from *B. tabaci*. Most specimens were mounted in Hoyer's medium, although a few were mounted in Canada Balsam. Measurements of type material were included for *E. strenua*, *E. bimaculata* and *E. protransvena*. The type material of *E. protransvena* is distorted, with measurements of the ovipositor most affected. Although this distortion greatly affected the univariate statistics, and hence their separation in the identification key, there was no overall affect on the placement of these specimens in the discriminant analyses. Measurements of the holotype of *E. armata* were initially included but they were very distinct from the other material and the data were removed from further analyses to prevent a general distortion of the results from the single specimen. Specimens were chosen that could be measured for all of the values so that missing values were not a part of the data set.

Size and shape differences were characterized by choosing 16 landmark points (black dots, Fig. 1) on the fore wing (1A, 5 points), gaster (1B, 3 points), mid tibia (1C, 2 points) and antenna (1D, 6 points). Measures of the apex of the fore wing could not be associated with specific structures and points were chosen by estimating the most apical point of the fore wing (FWL) and the greatest distance perpendicular to the anterior margin of the fore wing (FWW). The 10 measures (Fig. 1, Table 2) were selected as being appropriate for separating these and other species of *Encarsia*.

Specimens were measured using a Leica DMRB microscope at $78.8\times$ magnification. Point measures were taken using Morphosys (Meachum & Duncan 1987) through a Sony DXC-107 videochip camera. Reference coordinates were collected and converted to euclidean distances in

Table 1. *Encarsia* species and associated geographic and biological information used in the morphometric analysis. The host list is complete for the material available. Additional host records for *E. protransvena* include *Trialeurodes variabilis* on *Carica* (Caricaceae) and *Aspidiotus* on *Dioscorea* (probably erroneous). Questionable localities (possibly contaminated laboratory cultures) are marked by a double question mark.

<i>Encarsia</i>	Locality	n	Host species	Plant host
<i>E. bimaculata</i>	Hong Kong	2	<i>Bemisia tabaci</i>	<i>Hibiscus</i> (Malvaceae)
	India	3	<i>Bemisia tabaci</i>	<i>Hibiscus</i>
	India	25	<i>Bemisia tabaci</i>	culture
	Israel ??	5	<i>Bemisia tabaci</i>	culture
	Mexico ??	1	<i>Bemisia tabaci</i>	<i>Hibiscus</i>
	Philippines	13	<i>Bemisia tabaci</i>	<i>Solanum</i> (Solanaceae)
	Sudan ??	1	<i>Bemisia tabaci</i>	culture
	USA: Florida	3	<i>Bemisia tabaci</i>	<i>Hibiscus</i>
	USA: Florida	3	<i>Bemisia tabaci</i>	<i>Sesamum</i> (Pedaliaceae)
	USA: Florida	2	<i>Bemisia tabaci</i>	<i>Euphorbia</i> (Euphorbiaceae)
	USA: Texas	5	<i>Bemisia tabaci</i>	culture
<i>E. citri</i>	Japan	12	<i>Dialeurodes citri</i>	<i>Citrus</i> (Rutaceae)
<i>E. neocala</i>	New Caledonia	15	<i>Orchamplatus</i> sp.	<i>Citrus</i>
<i>E. protransvena</i>	Colombia ??	2	<i>Dialeurodes citrifolii</i>	<i>Citrus</i>
	Grand Cayman	2	<i>Dialeurodes citrifolii</i>	<i>Citrus</i>
	USA: Florida	1	black whitefly	<i>Liquidambar</i> (Hamamelidaceae)
	USA: Florida	2	<i>Dialeurodes citri</i>	<i>Ligustrum</i> (Oleaceae)
	USA: Florida	5	<i>Dialeurodes citri</i>	<i>Melia</i> (Meliaceae)
	USA: Florida	3	<i>Dialeurodes citri</i>	<i>Citrus</i>
	USA: Florida	21	<i>Dialeurodes citrifolii</i>	<i>Dioscorea</i> (Dioscoreaceae)
	USA: Florida	3	<i>Dialeurodes citrifolii</i>	<i>Citrus</i>
	USA: Florida	3	<i>Dialeurodes kirkaldii</i>	<i>Jasminum</i> (Oleaceae)
	USA: Florida	1	<i>Dialeurodes</i> sp.	<i>Jasminum</i>
	USA: Florida	1	<i>Trialeurodes abutilonia</i>	<i>Solanum</i> (Solanaceae)
	USA: Georgia	4	<i>Dialeurodes citri</i>	<i>Jasminum</i>
	USA: Georgia	3	<i>Bemisia tabaci</i>	<i>Gossypium</i> (Malvaceae)
	USA: Georgia	4	<i>Bemisia tabaci</i>	<i>Hibiscus</i>
	USA: Mississippi	1	<i>Bemisia argentifolia</i>	<i>Abelmoschus</i> (Malvaceae)
	USA: Mississippi	3	<i>Bemisia argentifolia</i>	<i>Cleome</i> (Capparaceae)
	Puerto Rico	19	<i>Dialeurodes citrifolii</i>	<i>Citrus</i>
	Puerto Rico	1	<i>Dialeurodes citri</i>	<i>Citrus</i>
	Puerto Rico	1	<i>Parlatoria ziziphi</i> *	<i>Citrus</i>
	Spain	2	<i>Parabemisia myricae</i>	unknown
<i>E. strenua</i>	China: Guangzhou	1	<i>Dialeurodes</i> sp.	<i>Citrus</i>
	Hong Kong	2	<i>Dialeurodes kirkaldii</i>	<i>Jasminum</i>
	Hong Kong	1	<i>Bemisia giffardii</i> (HT)	unknown
	India	15	<i>Dialeurodes citri</i>	<i>Citrus</i>
	USA: California	5	<i>Parabemisia myricae</i>	<i>Citrus</i>

* Probably a wrong association (Diaspididae).

Morphosys, and analyzed using the statistical analysis system (SAS, Version 6.12) software. Principle component analysis (PCA) was performed on the variance-covariance matrix for the 10 variables formed from the logarithms (base 10) of the raw data. PCA was performed to ob-

serve the distribution of observations without the *a priori* constraints of assigning them to a particular species (class). Canonical variates analysis (CVA) was used to evaluate variables for the discrimination of individuals using the five species as class variables in the analysis. In all cas-

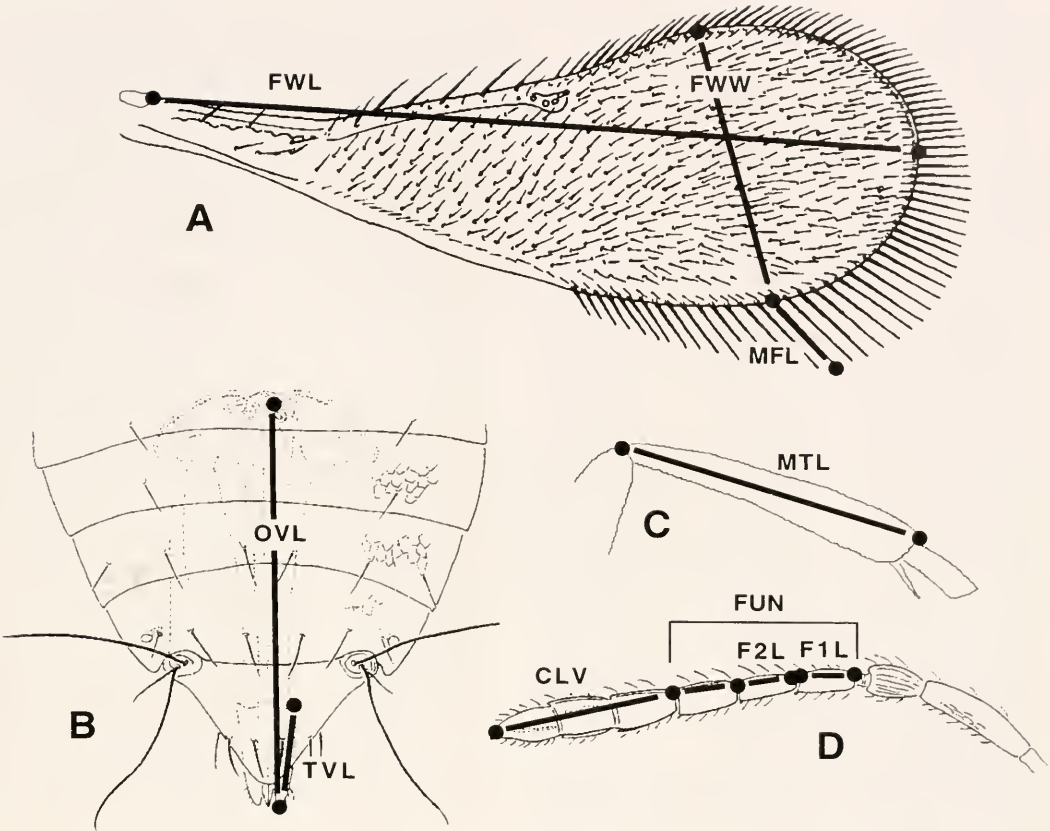


Fig. 1. Measurements of female *Encarsia* for morphometric analysis. Dots are landmark points, the coordinates of which were recorded in Morphosys; heavy lines are calculated distances. (A) fore wing, (B) gaster, (C) mid tibia, (D) antenna.

es, analysis of the raw data was virtually the same as the log-transformed data but only the latter is presented. Homogeneity of the covariance matrices of the five clas-

ses was rejected ($P < 0.0001$, $\chi^2 = 405.05$, 220 df); therefore within class rather than pooled covariance matrices were used. The data sets and a list of locality and host

Table 2. Description of distances measured for morphometric analyses.

Abbreviation	Character	Description
FWL	Fore wing length	Maximum length from apex of humeral plate to wing apex.
FWW	Fore wing width	Maximum width measured perpendicular to fore wing margin.
MFL	Marginal fringe length	Length of fringe seta at posterior wing margin.
OVL	Ovipositor length	Length from proximal margin of basal ring to extreme apex.
TVL	Third valvula length	Maximum lateral length.
MTL	Metatibial length	Maximum dorsal length.
CLV	Clava length	Maximum dorsal length.
FUN	Funicle length	Maximum dorsal length (excluding anellus).
F1L	Flagellomere 1 length	Maximum dorsal length.
F2L	Flagellomere 2 length	Maximum dorsal length.

information is available from the authors upon request.

RESULTS

Two distinct clusters of species were apparent from our initial observations of specimens, although these can be difficult to separate on the basis of one or even a few absolute characteristics. *Encarsia strenua* and *E. neocala* have a proportionally longer ovipositor in relation to body size than do *E. bimaculata*, *E. citri* and *E. protransvena*. Although this characteristic is usually distinct, a number of specimens fall into a gray zone in which making an accurate decision is difficult. Within each cluster, species are also difficult to separate because of few clearly defined or absolute characteristics. *Encarsia protransvena* and *E. citri* have been considered as the same species in the past (Polaszek *et al.* 1992), but characteristics of the third valvula (angulate with a prominent lateral seta in *E. citri*) suggest they are distinct species, but again, no single measurement or ratio provides absolute separation of all individuals. Females of *Encarsia bimaculata* are easily distinguished from other species in the analysis by their predominantly dark color (usually a feature of males) and much shorter ovipositor to clava ratio (1.33–1.78 versus greater than 2.0 in the other species), but otherwise they are very similar to *E. protransvena*.

The host ranges for each *Encarsia* species vary from very specific to polyphagous (Table 1). For *E. citri* and *E. neocala*, host specificity may be a product of geographic isolation and limited host availability. For example, a laboratory culture of *E. citri* has been reared successfully for a few years on *Bemisia argentifolii* Bellows & Perring (Bellows, pers. comm.; cultures verified by Heraty & Polaszek). However, *Encarsia bimaculata* has a broad geographic host range and has been reared only from one (*B. argentifolii*, but possibly also *B. tabaci*) species of *Bemisia* (Table 1). Both *E. bimaculata* and *E. protransvena* are sympat-

ric and usually occur in different hosts (*Bemisia* versus *Dialeurodes*), although both have been reared from *Bemisia*. Some species are polyphagous. *Encarsia protransvena* were reared from seven different host species in four genera, and in many cases, were reared from different host species at the same locality. The two specimens of *E. protransvena* reared from *Parabemisia* in Spain represent a substantial departure in both host and range, but these specimens clustered for all of the following measurements and comparisons with other *E. protransvena*. Interestingly, it had been a single odd specimen, a dark female of *Encarsia transvena* from Florida (females normally completely yellow), that had raised our initial suspicions about whether *E. bimaculata* was merely a dark form of *E. protransvena*, and prompted this study.

Univariate and Bivariate Analysis.—Univariate measures, along any particular axis, are either overlapping or very marginally separate species (Table 3), exemplifying the problems associated with separating species by individual measures. Although certain species can be clearly separated, there is a narrow zone of overlap, at least in size, for the pairs of species we would consider as closely related (*E. neocala* and *E. strenua*, *E. protransvena* and *E. citri*). Of the two groups initially recognized (*E. bimaculata*, *E. citri* and *E. protransvena* versus *E. strenua* and *E. neocala*), the ratio of ovipositor length to mid tibial length (OVL/MTL) is probably the best means of separation (Table 4). The overlap in the range of OVL/MTL for *E. protransvena* with *E. strenua* and *E. protransvena* is primarily the result of distortions in the type material; only one paratype specimen exceeds a ratio of 1.58, and only five specimens, including the two paratypes, exceed a ratio of 1.55, which is less than any of the *E. strenua* or *E. neocala*. No other measures by themselves distinguished the two groups. Since not all specimens can be mounted perfectly, any separation based only an OVL/MTL ratio of more or less

Table 3. Univariate statistics for variables in the morphometric analyses of *Encarsia* data set. Variables are means (standard deviation) over range in millimeters.

Variable	<i>bimaculata</i>	<i>protransvena</i>	<i>citri</i>	<i>strenua</i>	<i>neocala</i>
n	61	83	12	24	15
FWL	0.48 (0.04) 0.34–0.54	0.60 (0.07) 0.48–0.75	0.77 (0.06) 0.65–0.85	0.73 (0.70) 0.61–0.82	0.55 (0.04) 0.50–0.63
FWW	0.16 (0.02) 0.12–0.20	0.21 (0.03) 0.16–0.28	0.31 (0.02) 0.26–0.35	0.28 (0.03) 0.02–0.33	0.23 (0.02) 0.21–0.27
MFL	0.07 (0.01) 0.06–0.08	0.06 (0.01) 0.05–0.07	0.07 (0.01) 0.06–0.08	0.06 (0.01) 0.04–0.07	0.05 (0.01) 0.04–0.06
OVL	0.02 (0.02) 0.15–0.23	0.30 (0.03) 0.22–0.37	0.34 (0.02) 0.28–0.36	0.47 (0.05) 0.35–0.55	0.30 (0.03) 0.27–0.34
TVL	0.06 (0.00) 0.05–0.07	0.08 (0.01) 0.05–0.11	0.09 (0.01) 0.08–0.10	0.14 (0.02) 0.11–0.16	0.10 (0.01) 0.08–0.12
MTL	0.16 (0.01) 0.12–0.18	0.21 (0.03) 0.16–0.27	0.26 (0.02) 0.22–0.28	0.27 (0.03) 0.21–0.32	0.18 (0.02) 0.16–0.21
CLV	0.13 (0.01) 0.10–0.15	0.13 (0.01) 0.09–0.15	0.16 (0.01) 0.14–0.17	0.16 (0.01) 0.13–0.17	0.13 (0.01) 0.12–0.14
FUN	0.12 (0.01) 0.08–0.14	0.14 (0.02) 0.10–0.17	0.19 (0.01) 0.17–0.21	0.18 (0.02) 0.15–0.20	0.12 (0.01) 0.10–0.14
FIL	0.04 (0.00) 0.03–0.05	0.05 (0.01) 0.03–0.06	0.06 (0.01) 0.05–0.07	0.06 (0.01) 0.04–0.07	0.04 (0.01) 0.03–0.05
F2L	0.04 (0.01) 0.02–0.05	0.05 (0.01) 0.03–0.06	0.07 (0.00) 0.02–0.05	0.06 (0.01) 0.04–0.06	0.04 (0.01) 0.03–0.05

than 1.55 may fail and other measures or characteristics are necessary.

Through combinations of variables, more distinctive nonoverlapping differences occur. *Encarsia bimaculata* are distinct from *E. citri* in all bivariate plots (Fig. 2). *Encarsia protransvena* show some overlap with *E. bimaculata* and *E. citri* in most plots, with *E. citri* most distinct for OVL/CLV (Fig. 2B), OVL/FUN (Fig. 2C) and TVL/FUN (Fig. 2D) and *E. bimaculata* most distinct for OVL/CLV (Fig. 2B) and

OVL/FUN (Fig. 2C). In no case is there a clear, non-overlapping, separation of these species based on either univariate statistics (Table 2) or, with the exception of OVL/CLV for *E. bimaculata*, the ratios formed by each of these combinations (Table 4). The noticeable overlap between *E. neocala* and *E. protransvena* for some characters (Figs. 2: B, C) can be dismissed by other more distinctive morphological characteristics (dark pronotum, broader fore wing, longer ovipositor). *Encarsia neo-*

Table 4. Range of ratio measures for the combinations of features represented in Figure 1.

Ratio	<i>bimaculata</i>	<i>protransvena</i>	<i>citri</i>	<i>strenua</i>	<i>neocala</i>
FWL/FWW	2.58–2.99	2.62–3.11	2.39–2.68	2.44–2.67	2.32–2.44
OVL/CLV	1.33–1.78	2.00–3.37	2.00–2.34	2.43–3.26	2.16–2.56
OVL/FUN	1.52–1.94	1.85–2.85	1.63–2.01	2.35–2.89	2.39–2.76
TVL/FUN	0.43–0.59	0.40–0.79	0.42–0.54	0.70–0.89	0.72–0.98
TVL/OVL	0.25–0.36	0.19–0.32	0.24–0.30	0.27–0.34	0.29–0.38
OVL/MTL	1.09–1.38	1.29–1.74	1.22–1.35	1.56–1.97	1.60–1.79

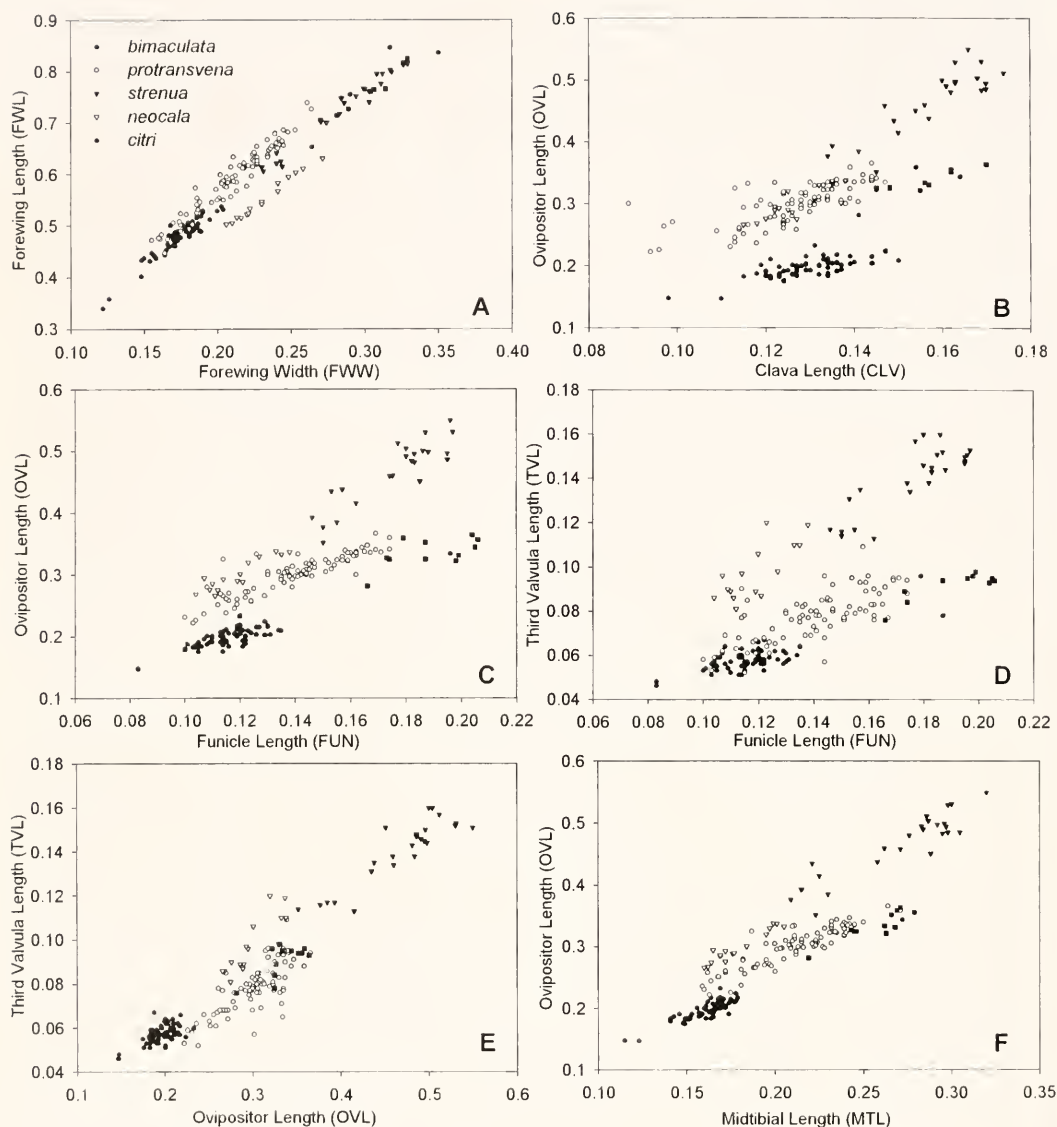


Fig. 2. Two-variable scatterplots for the five species of *Encarsia*. All measurements in mm.

cala and *E. strenua* are clearly separated from each other on all of the bivariate plots (Fig. 2), although for ratio comparisons, they are distinct, but overlapping, only for FWL/FWW (Table 4). In all cases, the five specimens of *E. strenua* reared from *Parabemisia* in California were smallest in size for most characteristics, usually forming a distinct cluster isolated from the majority of the southeast asian *E. strenua* (Fig. 2).

Bivariate plots of the variables which best discriminate the species of *Encarsia* (Fig. 2), in general, demonstrate a strong positive correlation based on size. Fore wing length and width (Fig. 2A) have the most direct linear association. Size variation of the host whiteflies does appear to have an effect on parasitoid size: *Bemisia* consistently yielded the smallest parasitoids (*E. bimaculata* and *E. protransvena*), *Parabemisia* yielded moderately-sized wasps

(*E. protransvena* and *E. strenua*), and *Orchamoplatus* yielded intermediate sized wasps (*neocala*). *Dialeurodes*, however, yielded almost the entire range of sizes found in *E. citri*, *E. protransvena* and *E. strenua*. Within *Dialeurodes*, *D. citri* and *D. kirkaldii* yielded the complete range of size variants for both *E. protransvena* and *E. strenua*; *E. protransvena* reared from *D. citrifolii* had a similar range of size variants, but only within the bounds of that species.

Principal Components Analysis.—Individual specimens of the five species are projected on the first two principal components, which accounted for 92.6% of the overall variance (Fig. 3). The first principal component (PCI) accounts for 84.4% of the variance. Even with log-transformed data, size has an obvious impact on the distribution of points along PCI with the smallest species, *E. bimaculata*, having strong negative values along PCI and the larger species, *E. citri* and *E. strenua*, having strong positive values along PCI. Eigenvalues and weights for the first two components are presented in Table 5. Marginal fringe length (MFL) had almost no contribution to PCI. This absence of any correlation was reflected in a bivariate plot of MFL against FWL, which showed almost no correlation within species; a rather surprising result considering the importance of the relative length of the MFL in *Encarsia* taxonomy. Along PCI, the other variables had approximately equal contributions, although measurements of the ovipositor (OVL, TVL) had the largest influence. Along PCII, the marginal fringe (MFL), ovipositor (OVL, TVL) and antenna (FUN, F1L, F2L) had the greatest influence.

Five distinct clusters, representing the five species, occur within the first two principal components of the log-transformed data (Fig. 3). *Encarsia protransvena* had the greatest scatter of points and overlaps minimally with *E. neocala*, *E. bimaculata* and *E. citri*, but not at all with *E. strenua*. Considering that there are no *a priori*

assumptions of group membership, we regard the clustering of points as a strong indicator of their group membership. Each overlapping group was clearly distinguished on examination of the third principal component.

A principal components analysis of only *E. protransvena*, using either host or locality as *a priori* groups, failed to separate out any meaningful clusters along the first three principal components.

Canonical Variates Analysis.—Individual specimens are projected along the first two canonical variates (CVI & CVII) of the log-transformed data, which account for 89.3% of the original variance (Fig. 4). The five species are clearly discriminated, however no species can be completely separated along the first canonical variate and only *E. neocala* can be clearly separated along the second. Although *E. citri* appears to overlap with *E. bimaculata* and *E. protransvena*, it is very clearly discriminated on a projection of the second and third canonical variate. The points for *E. citri* are in a plane clearly behind (class mean of -4.32 along CVIII; Table 6) those of *E. bimaculata* ($\bar{x} = 0.88$) and *E. protransvena* ($\bar{x} = -0.37$). The single specimen of *E. bimaculata* that appears to overlap the *E. citri* cluster along CVI and CVII is part of a long series reared from *Bemisia* in India. This specimen has a longer ovipositor (0.233 mm) than other *E. bimaculata* but, although it is an outlier on all of the bivariate plots, it is not distinct from the main cluster and is never included in the *E. citri* group in the univariate comparisons (Fig. 2). Also, the score for the specimen along CVIII (1.34) is about average from other *E. bimaculata* and very distinct from *E. citri* (-4.98 to -3.52). *Encarsia protransvena* and *E. citri*, which are difficult to separate on univariate characteristics, very marginally overlap on CVI & CVII; the clusters for each are distinct along CVII & CVIII, but with an overlap of scores along each variate. Notably, *E. strenua* and *E. neocala* are clearly separated on both CVI

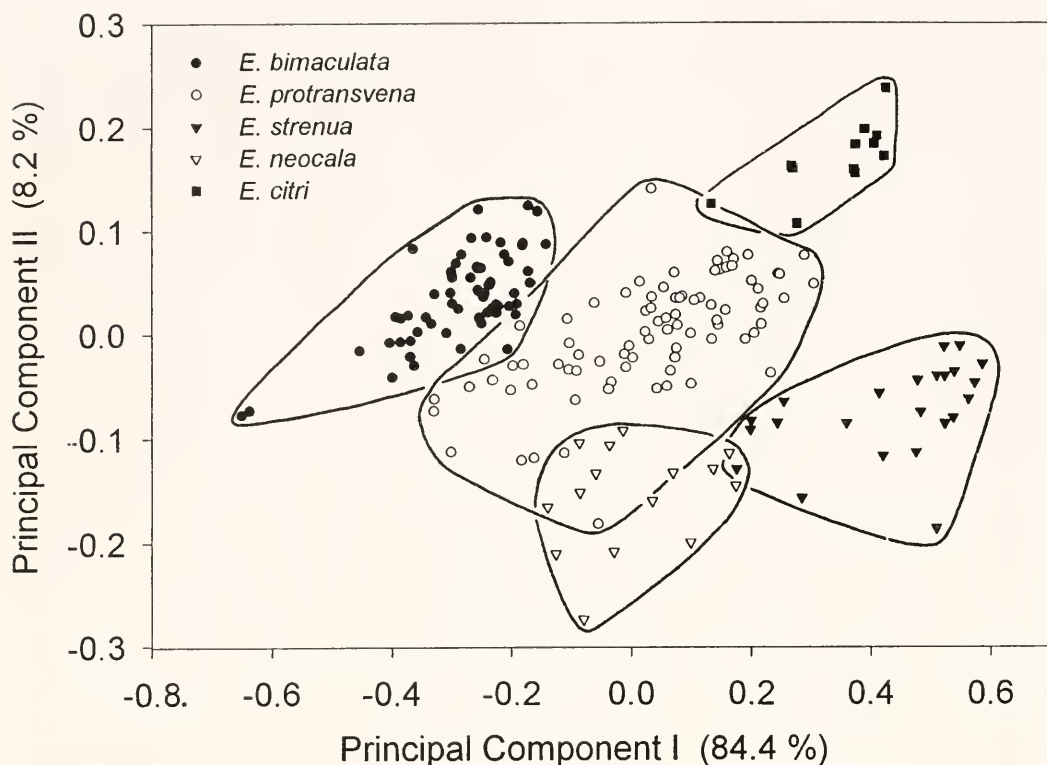


Fig. 3. Plot of the first two principal components from the principal components analysis of the log-transformed data set. The first principal component contains 84.4% of the sample variance, the second principal component contains 8.2%. Artificial boundaries define the limits of *a priori* groups.

& CVII (Fig. 4) and CVII & CVIII, with the majority of separation in both cases occurring along CVII (Table 6). A reclassification of individuals using the discriminant

functions resulted in 100% allocation to the correct *a priori* grouping. Stepwise discriminant analysis failed to identify any variables that could be excluded and still provide accurate classification of all specimens.

The standardized and raw coefficients for the log-transformed data are presented in Table 6. The standardized coefficients represent the amount that the canonical variate will change for each change in the original variable by one standard deviation (Woolley & Browning 1987). Larger coefficients are generally better characters for discriminating points along that particular analysis. Characteristics of the ovipositor (OVL) and fore wing (FWL, FWW) had the strongest contribution along the first variate (CVI). These were also ranked as the best variables for discrimination in

Table 5. Eigenvalues and weights for the first two principal components, computed from the covariance matrix of the log-transformed data.

Variable	PCI	PCII
Eigenvalue	0.073	0.007
Proportion of Variance	0.844	0.082
FWL	0.28	0.14
FWW	0.32	0.09
MFL	-0.06	0.46
OVL	0.45	-0.34
TVL	0.44	-0.55
MTL	0.32	0.11
CLV	0.14	0.16
FUN	0.30	0.29
FIL	0.33	0.30
F2L	0.31	0.37

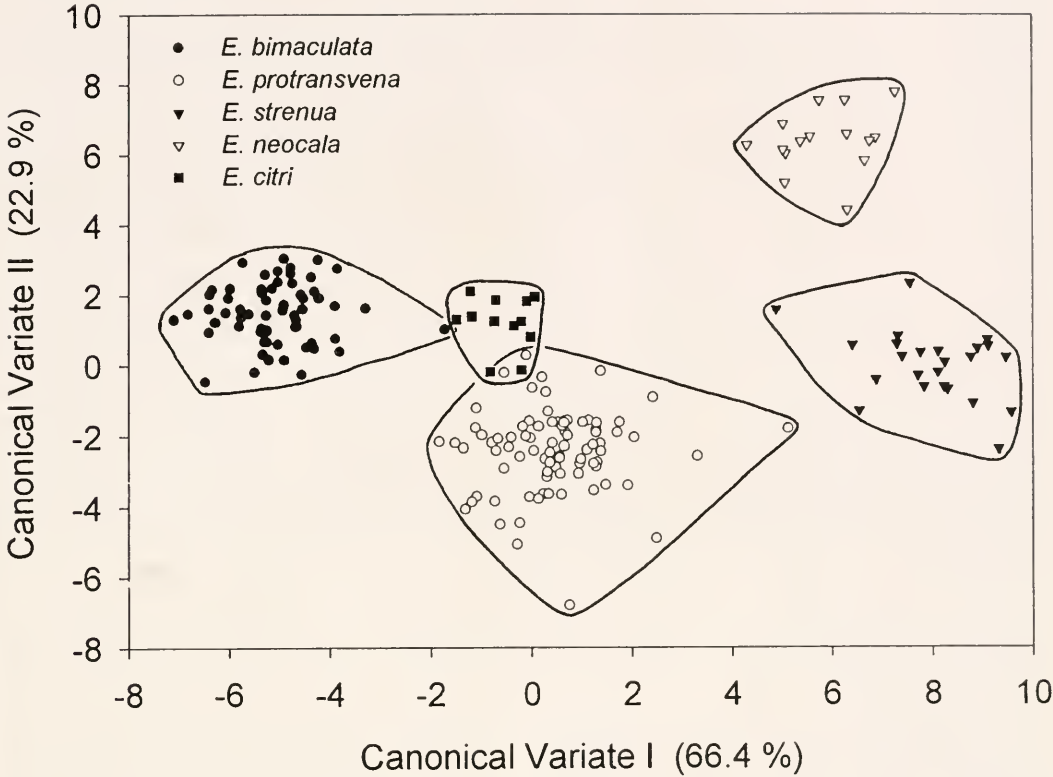


Fig. 4. Plot of the first two canonical variates from the canonical variates analysis of the log-transformed data set. The first canonical variate contains 66.4% of the sample variance, the second canonical variate contains 22.9%. Artificial boundaries define the limits of *a priori* groups.

the stepwise analysis. Of the two most substantial features, *E. strenua* and *E. neocala* have a proportionally longer ovipositor, as already noticed, and *E. bimaculata* has a proportionally shorter fore wing. Length of the metatibia (MTL) and, again, the fore wing (FWL, FWW) were strong contributors to the second canonical variate.

A canonical variates analysis of only *E. protransvena*, using either host or locality as reference criteria, failed to separate out any meaningful clusters in different ordinations of the first three canonical variates. The only segregation using host as a class criterion was along the first canonical variate, with individuals reared from *Bemisia* mostly negative (canonical scores below 0) and individuals from all of the other whitefly species mostly positive (scores

greater than -1). *Bemisia* are smaller than the other whiteflies, and this likely represents segregation by size. Using geographical locality as the class criterion, there was no meaningful segregation of clusters by locality along any axes; the only segregation of clusters was again host related, corresponding to species reared from *Bemisia* versus other whiteflies along the first canonical variate. The error rate for reclassifying the observations was 23.9% for all observations and 56.4% for specimens from Florida (n = 39).

DISCUSSION

Our initial grouping of species is supported by the distinct clustering of groups found using either principal components or canonical variates analysis. Most of the specimens were segregated along the first

Table 6. Standardized and raw coefficients and class means for the canonical variates analysis. The rows have been sorted by the elements of the vector of standardized coefficients for the first canonical variable. Standardized coefficients are the amount that the canonical structure will change for a change in the original variable of one standard deviation.

Variable	Standardized coefficients			Raw coefficients		
	CV1	CV2	CV3	CV1	CV2	CV3
OVL	5.91	-1.88	0.36	46.81	-14.85	2.86
FWW	2.88	6.02	-1.53	31.64	66.04	-16.83
TVL	1.11	1.85	1.08	8.55	14.16	8.26
F1L	0.74	0.10	-0.62	0.77	1.09	-6.42
MFL	-0.01	-0.18	0.12	-0.21	-3.24	2.15
F2L	-0.28	0.10	-1.84	-3.03	1.12	-19.99
CLV	-0.57	0.68	1.19	-11.18	13.46	23.54
FUN	-0.75	-0.80	1.52	-8.79	-9.44	17.86
MTL	-1.40	-3.75	3.06	-15.59	-41.62	33.98
FWL	-3.31	-2.65	-3.42	-42.56	-34.06	-44.04
Species	Class means					
<i>bimaculata</i>	-5.08	1.49	0.88			
<i>protransvena</i>	0.45	-2.43	-0.37			
<i>citri</i>	-0.57	1.20	-4.32			
<i>strenua</i>	7.98	0.02	1.79			
<i>neocala</i>	5.84	6.39	-0.96			

two axes in both analyses, and any area of overlap was resolved along the third axis. The fact that all specimens could be correctly reclassified to their respective *a priori* groups is another indication of their distinctness. The complexity of the separation is, however, reflected by the inability to remove any of the variables to achieve complete reclassification.

Encarsia bimaculata is the most distinctive species in both color and morphology, and none of the analyses would support these as mere color variants of *E. protransvena*. Both *E. bimaculata* and *E. protransvena* are parasites of *Bemisia tabaci* *argenteifolii* in the same geographical region, and yet both maintain their morphometric integrity. *Encarsia citri* can be separated from *E. protransvena* by the structure of the third valvula and setae of the midlobe. These characters are subtle and may not be trustworthy. However, *E. citri* formed a morphometric grouping distinct from *E. protransvena* in all analyses. Again, both species use *D. citri* as a host but, even when using the same host, *E. citri* were consis-

tently larger in size for almost all features except ovipositor length. The separation of *E. citri* from *E. protransvena* in the morphometric analyses was along all three axes, suggesting that both size and shape contributed to the difference.

Encarsia protransvena were most variable for both size and host range. Hosts, which vary in size, have an obvious impact on size of the parasitoids. Specimens of *E. protransvena* reared from *Bemisia* were generally smaller for most features than those reared from other hosts. In the canonical variates analysis by host, the specimens reared from *Bemisia* were separated along the first axis, with highest weights applied to the length and width of the fore wing (shorter and broader in specimens reared from *Bemisia*), although this was barely noticeable in the bivariate plots and is here considered as inconsequential. The full range of size, from smallest to largest were found in specimens reared from *Dialeurodes*, and among these, *D. citri* yielded the largest size range. Whether the size range from *D. citri* is a result of parasitoids

emerging from different sized host or different instars is unknown.

Encarsia bimaculata, *E. citri*, *E. neocala* and *E. strenua* all have a southeast Asian origin. *Encarsia bimaculata* was purposefully introduced into Florida from India (Nguyen & Bennett 1995). *Encarsia strenua* was probably introduced into California from original material collected in India. Although material of *E. strenua* from India was reared in quarantine in Riverside, CA, in 1969, there is no record of a purposeful release of this species. The californian *E. strenua* was collected only between 1980 and 1982 at Tustin and the Irvine Ranch, both in Orange County, California. The origin of *E. protransvena* in the New World is more puzzling, especially as only two of the 40 species that we place in the *strenua* group are apparently endemic in the New World. *Encarsia protransvena* has been recorded primarily from the gulf coast states (Florida through Texas) and Puerto Rico, and from single rearings in Grand Cayman, Colombia (*D. citrifolii*), California (*D. citri*), and Honduras (*B. tabaci*) (Polaszek *et al.* 1992). The records from Central and South America and Grand Cayman all appear to be valid rearings from field collected material. The single record from California is probably from release efforts being undertaken at that time (Bellows, pers. comm.). For all of the bivariate and multivariate analyses, these odd rearings of *E. protransvena* clustered within the main group of specimens and are indistinguishable by any set of measurements from other *E. protransvena*. *Bemisia* and both species of *Dialeurodes* have been known from Florida since the early 1900's (Mound 1978; Nguyen *et al.* 1993), and yet no members of the *strenua* group were reared from whiteflies in any of these countries prior to 1984 (collection date of type material), even though there are several earlier collections of other species of *Encarsia* from whiteflies in Florida (Nguyen *et al.* 1993) and despite a renewed research program focusing on the

parasitoids of *Dialeurodes* in the late 1970's (Nguyen and Sailer 1979; Sailer *et al.* 1984). A collection of three specimens reared from *Parabemisia* in Valencia, Spain (included in the morphometric analyses), three specimens from China and Taiwan reared from *Dialeurodes* and *Aleurotrachelus* (Huang & Polaszek 1998), and one female from Egypt reared from *Dialeurodes* (Polaszek *et al.* 1999) are the only collections of *E. protransvena* from the Old World. Although from a unique host, the two specimens from Spain were certainly not unique morphologically and were about average (clustering centrally) for all bivariate and multivariate comparisons. The Egyptian specimen agrees in all characters with *E. protransvena*. The specimens from China and Taiwan were not part of this analysis, but exhibit diagnostic differences (see comments after description of *E. protransvena*) from the New World and Spain material that might suggest they could be a different species close to *E. protransvena* or *E. citri*. If *E. protransvena* did have an eastern Palearctic or southeast Asian origin, we expect that it would be more widespread as it is in the New World. However, the distribution and success of *E. protransvena* cannot be used to demonstrate its origin, and the evidence remains equivocal over the origin of *E. protransvena* in the southeastern United States as to whether it was accidentally introduced from the Old World (western Palearctic or southeast Asia) and became abundant in its new habitat, or if it spread northward from an origin in South America or the Caribbean. It might be interesting to postulate that the appearance of *E. protransvena* coincides with the apparent replacement of *Bemisia tabaci* with *B. argentifolii*, but the parasitoid also was found to be common on other genera of whiteflies in the same geographical range.

A discriminant function may be the best means of separating species such as *E. protransvena* and *E. citri*. However, in all cases, a majority of specimens can be suc-

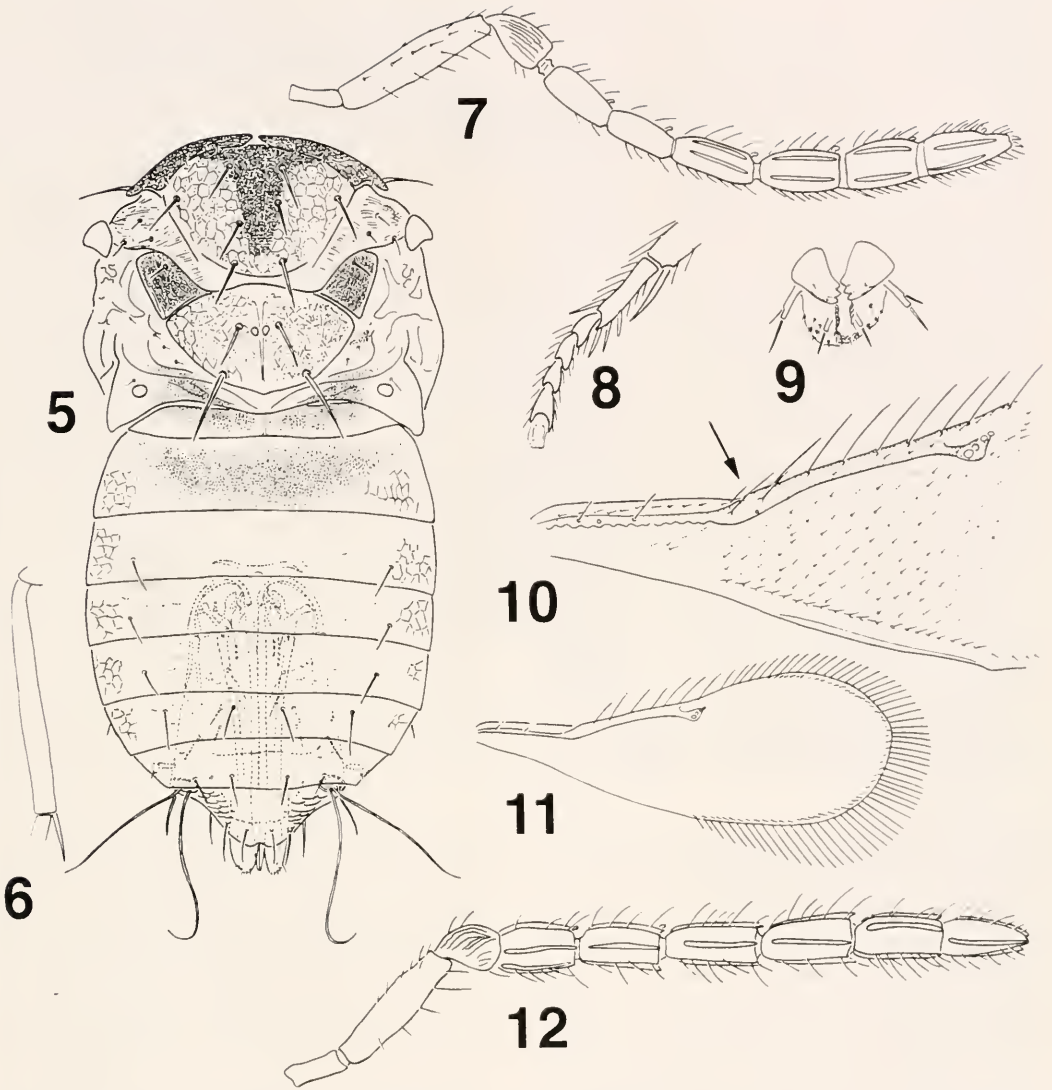
cessfully keyed using relatively straightforward measurements having a minimal amount of overlap, and any specimens within the zone of overlap can be segregated using other characters which may apply only to these specimens but not to

all of the specimens. Although still creating complex couplets, we feel that this would be the best means to painlessly separate species and is the method used in the accompanying identification key.

KEY TO FEMALES OF COMMONLY ENCOUNTERED SPECIES OF THE *STRENUA* GROUP

This identification key refers only to the species dealt with in this paper, a small representation of the 40 species that we have recently examined. It will, however, work for the species most commonly encountered in economically important crops. Members of the *strenua* group are recognized by having a combination of 2–3 marginal setae along the dorsal margin of the costal cell at the apex, a bare area just above the stigmal vein, and scutellar sensillae closely placed or touching.

1. Ovipositor almost as long as gaster, more than 1.56 times as long as middle tibia, if between 1.5 and 1.65 times then fore wing less than 2.6 times as long as broad. Ovipositor robust, tip often bent at an angle in slide-mounted specimens 2
 - Ovipositor clearly shorter than length of gaster, less than 1.5 times as long as middle tibia, some *E. protransvena* 1.5–1.6 times [deformed holotype 1.74 times], but then fore wing more than 2.67 times as long as broad [2.9 times in holotype of *E. protransvena*]. Ovipositor slender, tip always straight. 3
 2. Third valvula entirely yellow. Fore wing less than 2.44 times as long as broad and ovipositor less than 2.6 times as long as clava *E. neocala* Heraty and Polaszek, n. sp.
 - Third valvula dark brown at the extreme tip, otherwise yellow (Fig. 16). Fore wing more than 2.44 times as long as broad and ovipositor usually more than 2.7 times as long as clava, if shorter then fore wing more than 2.5 times as long as broad ... *E. strenua* (Silvestri)
 3. Metasomal tergite 7 (tergite with spiracles) with 4 setae, only 2 long setae medial to cerci (Fig. 29); ocellar triangle irregularly aciculate *E. sophia* (Girault) (= *transvena*)
 - M7 with 6 setae, 4 long setae medial to cerci (Fig. 27); ocellar triangle usually reticulate, if aciculate then with a different pattern [not all species included in this key] 4
 4. Body with extensive dark pigmentation (at least a large part of the mesoscutum, or two or more gastral tergites, dark) (Fig 5). Ovipositor less than 1.8 times as long as clava *E. bimaculata* Heraty and Polaszek n. sp.
 - Body, including antennae, almost entirely yellow. Ovipositor more than 2.0 times as long as clava 5
 5. Basal seta of third valvula long, exceeding base of subapical seta; subapical seta located half way between basal seta of third valvula and apex (Fig. 14). Midlobe of mesosoma usually with 5 pairs of setae, preapical pair overlapping or exceeding base of apical pair. Fore wing usually less than 2.6 times as long as broad (83.3% of specimens examined), if between 2.6 and 2.7 times, then clava more than 0.14 mm in length *E. citri* Ishii
 - Basal seta of third valvula not reaching base of subapical seta; subapical seta located beyond half way (0.65) between basal seta of third valvula and apex (Fig. 15). Midlobe of mesosoma usually with 4 pairs of setae, preapical pair not reaching base of apical pair. Fore wing usually more than 2.7 times as long as broad (92.8% of specimens examined), if between 2.6 and 2.7 times, then clava less than 0.14 mm in dorsal length *E. protransvena* Viggiani
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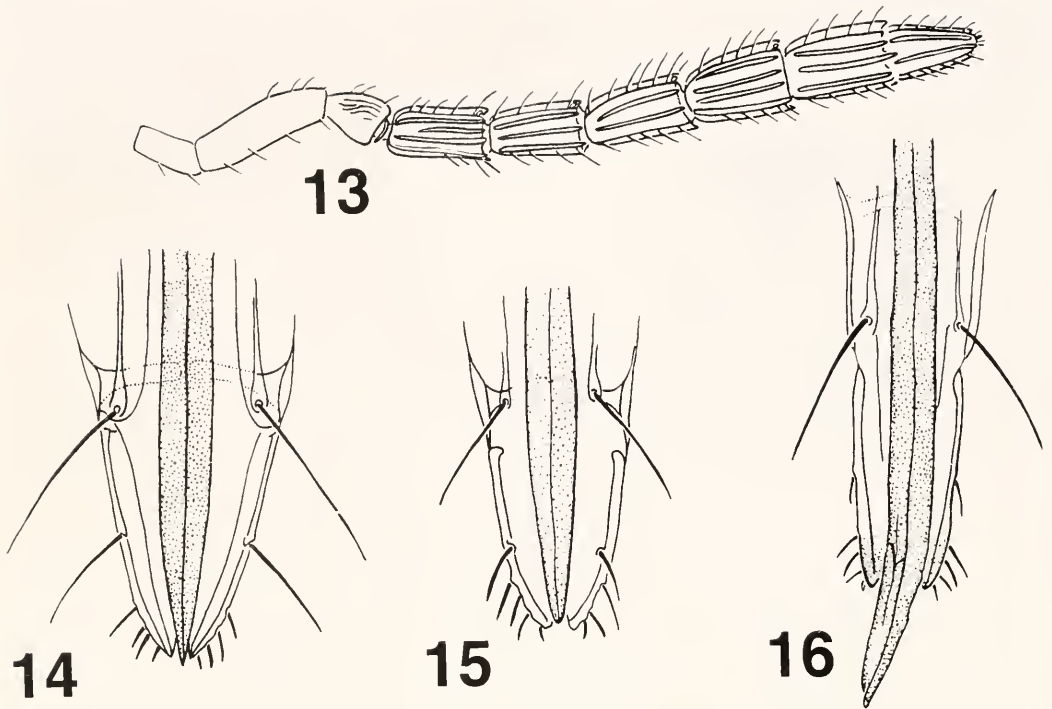


Figs. 5–12. *Encarsia bimaculata*: 5–11, female; 5, body; 6, mid tibia; 7, antenna; 8, mid tarsus; 9, mouthparts; 10, base of fore wing; 11, fore wing; 12, antenna of male. Arrow points to apical two costal cell setae diagnostic of the *strenua* group.

Encarsia bimaculata Heraty and
Polaszek, new species
(Figs. 5–12)

Female.—Antenna with 6 flagellomeres, clava 3-segmented; F1 2.0–2.2× as long as broad and as long as F3; antenna yellow basally, slightly darkened apically. Head confused transverse colliculate (as in fingerprint), ocellar triangle similar but sculpture somewhat areolate; yellow ex-

cept for a pale transverse band of brown across back of head; dorsal setae slight. Maxillary palpus 1-segmented. Mandibles 3/3 dentate, marginal teeth acute. Mesosoma mostly yellow except following which are brown: pronotum, midlobe of mesoscutum anteriorly and medially, tegula, axilla and propodeum submedially. Mesosoma with light hexagonally areolate sculpture dorsally; midlobe with 4 pairs of



Figs. 13-16. 13-14, *Encarsia citri*: 13, antenna of male; 14, third valvulae. 15, *Encarsia protransvena*, third valvulae; 16, *Encarsia strenua*, third valvulae.

setae, setae delicate and about equal in size, side lobe with 3 pairs, axilla with 2 pairs (lateral pair minute) and scutellum with 2 pairs. Scutellar sensillae ovoid and separated by less than their own maximum diameter; median groove usually narrow and distinct. Apical spur of mid tibia $0.6-0.8\times$ as long as basitarsus; basitarsomeres of midtarsus without pegs. Tarsal formula 5-5-5. Fore wing $2.58-2.99\times$ as long as broad, marginal fringe $0.25-0.36\times$ width of fore wing; disc uniformly setose; costal cell with row of 9-10 minute setae and with 1 long marginal setae apically; submarginal vein with 2 large setae, basal area with 5-6 setae posterior to submarginal vein; frenal fold with several prominent thornlike spines; wing mostly hyaline, weakly infuscate at base of submarginal vein and base of frenal fold. Metasoma mostly yellow, tergites I + II mostly brown, sometimes with faint medial spot on tergites V + VI; laterally

with weak cellulate reticulation; dorsal setal formula from tergite III: 2-2-2-6-6-6. Ovipositor $1.09-1.38\times$ as long as mid tibia, $1.33-1.78\times$ as long as clava, $0.6\times$ as long as gaster (base to tip of third valvula); third valvula stout, $1.6-2.2\times$ as long as broad, slightly extruded beyond epygium, entirely yellow.

Male.—Coloration similar to female but darker with entire metasoma brown, head with a transverse medial band of brown infuscation, and wings may be weakly infuscate in the basal half. Antenna with 6 flagellomeres, apical two flagellomeres fused, with segments distinctly separated (Fig. 12).

Comments.—This species is similar to *E. dialeurodis* Hayat for all features except for the darker coloration of the axillae, pronotum and mesoscutum (medially) (versus all yellow in *E. dialeurodis*) and F1 about equal in length to F2 (versus distinctly subequal). It is readily distinguished from

other species of the *strenua* group by the dark mesosomal coloration of females and the shorter ovipositor to clava ratio. The only noticeable difference in female coloration was a more extensive dark pigmentation of the metasoma in the specimens from Hong Kong, with gastral tergites V & VII almost completely dark; otherwise these did not differ from other specimens. Two smashed specimens from Thailand, one reared from *Bemisia tabaci* but with no other data, and the other from *Bemisia tabaci* on *Gossypium hirsutum* (Ban Ton Tea, 20.i.1992, F. Bennett 1224 [= *Encarsia* sp. in Nguyen & Bennett 1995]; both ♀ USNM), are identical for all characters of this species, except the ocellar triangle is transversely aciculate, the mandibles are less acutely toothed and the mid tibial spur is only 0.44× as long as the basitarsus. It is of interest that, assuming a random sampling, the original shipment of material of *E. bimaculata* from India (#1248) was only slightly biased for females (6:4), whereas, except for the Honduras lab culture (1:17), only two males have been discovered in all of the subsequent rearings. Another undescribed species in Florida (Gainesville; USNM) is very close, but it has a proportionally longer ovipositor (>2.0× as long as the clava), the female gaster is entirely dark, and the legs are also brown. This other species has also been reared from *Bemisia* and *Trialeurodes abutilonea*. *Encarsia bimaculata* is the *Encarsia* I [India], G [Guatemala] and S [Sudan] species released in Florida against *Bemisia argentifolia* (Nguyen & Bennet 1995).

Host.—Reared from *Bemisia argentifolia* and *B. tabaci* (Aleyrodidae).

Distribution.—India, Philippines, Thailand and USA (Florida, Texas?), and possibly Sudan, Israel and Mexico [possibly culture contaminations].

Material Examined.—Holotype, ♀, India: Tabarbhani, 19.vii.1994, culture in Gainesville, Florida, R. Nguyen, autoparasitoid, M92018. Deposited in USNM. Paratypes (80 females, 29 males): **Honduras**: lab culture [Florida] vi.1992, quarantine 1261 (1♀ 17♂ USNM). **Hong Kong**: Kowloon Park, 14.vii.1992, F.

Bennett Y944, *Bemisia tabaci* on *Chamaesyce? hirta* (2♀ USNM). **India**: same data as holotype (4♀, USNM, 7♀ 1♂ BMNH, 10♀ 1♂ UCRC); quarantine [Florida], 30.v.1991, R. Nguyen 903, 1065, 1248, *Bemisia tabaci* (6♀ USNM); Tabarbhani, 14.iv.1992, R. Nguyen, ex *Bemisia tabaci* on *Hibiscus* (3♀ USNM); lab culture [Florida] quarantine, original shipment 1248, 1992 (6♀ 4♂ USNM). **Philippines**: Benguet, 8.iii.1994, Legaspi, Carruthers, Poprawski, ex *Bemisia tabaci* on white potatoes, autoparasitoid, M94014 (11♀ UCRC, 5♀ BMNH); Quezon Dolores, 15.xii.1993, C. Moomaw, M93069, on eggplant (2♀ TAMU). **Israel**: [lab culture in Florida], R. Nguyen 1250, on *Bemisia tabaci* (7♀ 1♂ USNM). **USA**: Florida: Alachua Co., Gainesville, 7.ix.1992, F. Bennett Y935, *Bemisia tabaci* on *Euphorbia heterophylla* (2♀ 1♂ USNM); Alachua Co., Gainesville, 14.ix.1992, F. Bennett Y958, *Bemisia tabaci* on *Sesamum* (2♀ USNM); Alachua Co., Gainesville, 27.viii.1992, F. Bennett Y936, *Bemisia tabaci* on *Sesamum indicum* (2♀ 2♂ USNM); Alachua Co., Gainesville, 6.ix.1992, F. Bennett Y934, *Bemisia tabaci* on *Chamaesyce hirta* (3♀ 1♂ USNM); Hamilton Co., Jasper, 8.iv.1992, F. Bennett Y693, *Magnolia* sp. (1♂ USNM); Texas: Mission biological control laboratory (in culture from India), 16.xii.1993, M92018 (5♀ TAMU). **Mexico**: Taxco, 1992, P. Stansley 1292, *Bemisia tabaci* on *Chamaesyce hyssopifolia* (1♀ USNM). **Sudan**: [lab culture in Florida], 30.iv.1992, R. Nguyen 1249, on *Bemisia tabaci* (3♀ USNM). **Thailand**: xi.1977, G. Yonimoton [?], cotton (1♀ USNM).

Encarsia citri (Ishii)

(Figs. 13, 14)

Prospaltella citri Ishii, 1938: 29–30. Type data: Japan: Nagasaki. Syntypes, female. Type depository: National Institute of Agroenvironmental Sciences, Tsukuba, Japan. Described: female. Reared from *Dialeurodes citri*.

Encarsia strenua; Polaszek et al. 1992: 338. Incorrect synonymy.

Encarsia citri, Huang & Polaszek 1998: 352. Revised status.

Female.—Antenna with 6 flagellomeres, clava 3-segmented; F1 2.4–3.0× as long as broad and 0.9× as long as F3; antenna very pale brown, contrasting in color to rest of the body which is yellow. Vertex weakly areolate to colliculate, ocellar triangle weakly areolate; dorsal setae stout. Maxillary palpus 1-segmented. Mandibles chisel-shaped or very weakly 3/3 dentate, apical margin nearly flat. Mesosoma with weak hexagonally areolate sculpture dor-

sally; midlobe with 5 pairs of setae (rarely 6 pairs), posterior and lateral setae only slightly stouter than medial setae, side lobe with 3 pairs, axilla with 2 pairs (lateral pair minute), and scutellum 2 pairs, medial pair lateral to sensillae. Scutellar sensillae ovoid and separated by less than their own maximum diameter (rarely by a full diameter); median groove distinct. Apical spur of mid tibia $0.7\text{--}0.8\times$ as long as basitarsus; basitarsomere of midtarsus with 2–3 strong pegs, tarsomeres 3–5 each with 1 apical peg. Tarsal formula 5–5–5. Fore wing $2.39\text{--}2.68\times$ as long as broad, marginal fringe $0.18\text{--}0.25\times$ width of fore wing; disc uniformly setose; costal cell with row of 15–19 small setae and 2–3 long marginal setae apically; submarginal vein with 2 (rarely 3 on one side) large setae, basal area with 7–9 setae posterior to submarginal vein; frenal fold with several minute thornlike spines; wing hyaline. Metasoma yellow; laterally with weak cellulate reticulation; dorsal setal formula from tergite III: 2-2-2-6-6-6. Ovipositor $1.22\text{--}1.34\times$ as long as mid tibia, $2.00\text{--}2.34\times$ as long as clava, $0.5\text{--}0.6\times$ as long as metasoma (base to tip of third valvula); third valvula stout (Fig. 14), $1.26\text{--}1.95\times$ as long as broad, barely, if at all, extruded beyond epigium, entirely yellow.

Male.—Overall coloration pale brown, darker brown pattern on head and mesosoma similar to *E. bimaculata* female, gaster entirely brown. Setation pattern of mesosoma and metasoma as in female; some males with fewer setae in basal area (13) or fore wing and costal cell (4). Basitarsomere of middle leg with only 2 pegs. Antenna with 5 flagellomeres, apical two flagellomeres (5&6) fused, with segments distinguished only by a break in the pattern of linearia (Fig. 13).

Comments.—The shape and setation of the third valvula are distinct among all members of the *strenua* group. This species is most easily confused with *E. protransvena* but can be separated by the fea-

tures outlined in the key and usually the presence of 5 pairs of setae on the midlobe of the mesoscutum (versus 4 pairs).

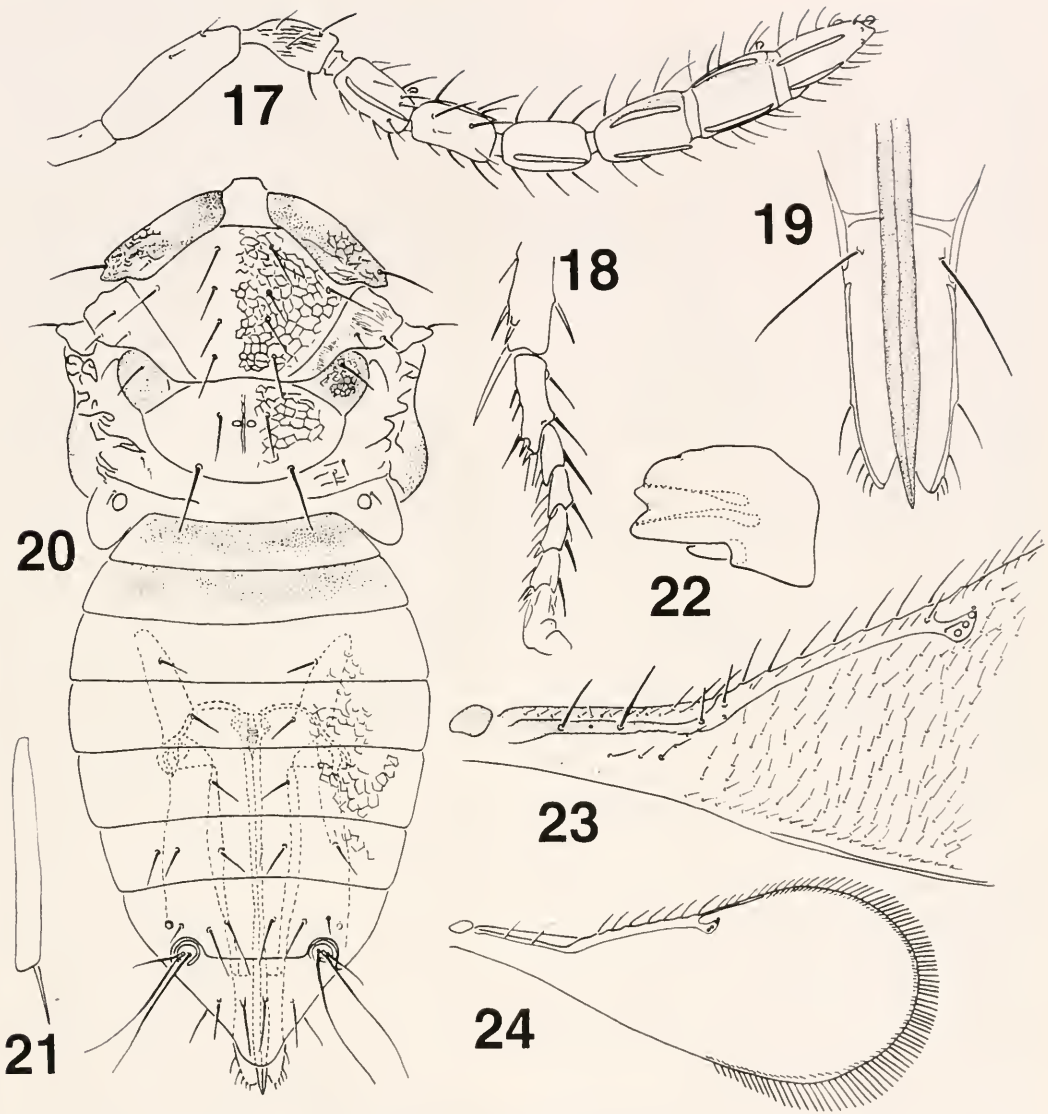
Hosts.—**Aleyrodidae**: *Dialeurodes citri* (Ashmead) (Ishii 1938).

Distribution.—**Palaeartic**: Japan (Ishii 1938).

Material Examined (6 males, 12 females).—**Japan**: Kyushu: Kagoshima City, 2.v, 15.vii.1970, S. Ohga, R70-31, R72-36, *Dialeurodes citri* on *Citrus* spp. (12♀ 4♂ 1 pupa UCRC); Kagoshima, Tareman, 18-19.viii.1972, S. Ohga, R72-50 (2♂ UCRC [with 2♂ of *E. transvena* on same slide]); Fukuoka, Tsuyazaki, 4.viii.1995, H. Kajita, ex *Dialeurodes citri* on *Citrus* (2♀ BMNH).

***Encarsia neocala* Heraty and Polaszek,
new species
(Figs. 17–24)**

Female.—Antenna with 6 flagellomeres, clava 3-segmented; F1 $1.6\text{--}1.9\times$ as long as broad and $0.8\text{--}1.0\times$ as long as F3; antenna yellow basally, darkened beyond or including pedicel. Vertex confused transverse colliculate, ocellar triangle similar but sculpture somewhat areolate; head yellow except for weak infuscation on inner margins of ocelli; dorsal setae slight. Maxillary palpus 1-segmented. Mandibles 2/2 or 3/3 dentate, ventral teeth acute, dorsal tooth blunt or rounded and often not apparent. Mesosoma mostly yellow except pronotum brown and axillae and propodeum laterally pale brown. Mesosoma with light hexagonally areolate sculpture dorsally; midlobe with 4–5 pairs of setae, posterior and lateral setae only slightly stouter than medial setae, side lobe with 3 pairs, axilla with 2 pairs (lateral pair minute), and scutellum 2 pairs, medial pair lateral to sensillae. Scutellar sensillae ovoid and separated by less than their own maximum diameter; median groove narrow and distinct. Apical spur of mid tibia $0.8\text{--}1.0\times$ as long as basitarsus; basitarsomere of midtarsus with 2–4 strong pegs, tarsomeres 4 and 5 each with 1 apical peg. Tarsal formula 5–5–5.



Figs. 17–24. *Encarsia neocala*, female: 17, antenna; 18, midtarsi; 19, third valvulae; 20, body; 21, mid tibia; 22, mandible; 23, base of fore wing; 24, fore wing.

Fore wing 2.32–2.44× as long as broad, marginal fringe 0.29–0.38× width of fore wing; disc uniformly setose; costal cell with row of 12–16 small setae and 2–4 long marginal setae apically; submarginal vein with 2 large setae, basal area with 4–5 setae posterior to submarginal vein; frenal fold with several minute thornlike spines; wing mostly hyaline, weakly infuscate at base of submarginal vein. Me-

tasoma mostly yellow, tergites I + II usually brown, sometimes almost completely yellow; laterally with weak cellulate reticulation; dorsal setal formula from tergite III: 2-2-2-6-6-6. Ovipositor 1.60–1.79× as long as mid tibia, 2.16–2.56× as long as clava, 0.7× as long as metasoma (base to tip of third valvula); third valvula elongate (Fig. 19), 2.6–3.0× as long as broad, extruded beyond epygium, entirely yellow.

Male.—Unknown.

Comments.—The longer third valvulae, longer ovipositor relative to gaster length, and stouter ovipositor (indicated by a tendency for the tip to be bent in slide mounts) place this species as similar to *E. strenua*. However, in *E. neocala* the third valvula is entirely yellow (versus tipped brown in *E. strenua*), the midlobe of the mesoscutum is entirely yellow with the axillae slightly darker (versus entirely yellow or the midlobe slightly darkened anteriorly in *E. strenua*), fewer setae in the costal cell, and the ocellar triangle more weakly sculptured.

Host.—Reared from *Orchamoplatus caledonicus* (Dumbleton) (Aleyrodidae) [reads *Orchamnus neocaledonicus* on label] on *Citrus*.

Material Examined.—Holotype, ♀, New Caledonia, Nouméa, 10.ix.1970, G. Fadres, ex [*Orchamnus neocaledonicus*]. Deposited in USNM. Paratypes (37 females): same data, (5♀ USNM, 5♀ BMNH, 27♀ UCRC).

Encarsia protransvena Viggiani

(Figs. 15, 25–28)

Encarsia protransvena Viggiani, 1985a: 89–90.

Type data: USA: FL, Broward Co., Fort Lauderdale. Holotype female, by original designation. Type depository: IEUN. Described: female. Illust. Reared from *Dialeurodes kirkaldii*. Placed in *strenua* group by Hayat (1989).

Encarsia strenua; Polaszek et al. 1992: 388. Described: female. Illust. (in part).

Encarsia strenua; Schauff et al. 1996: 29. Described: female. Illust. Misidentification.

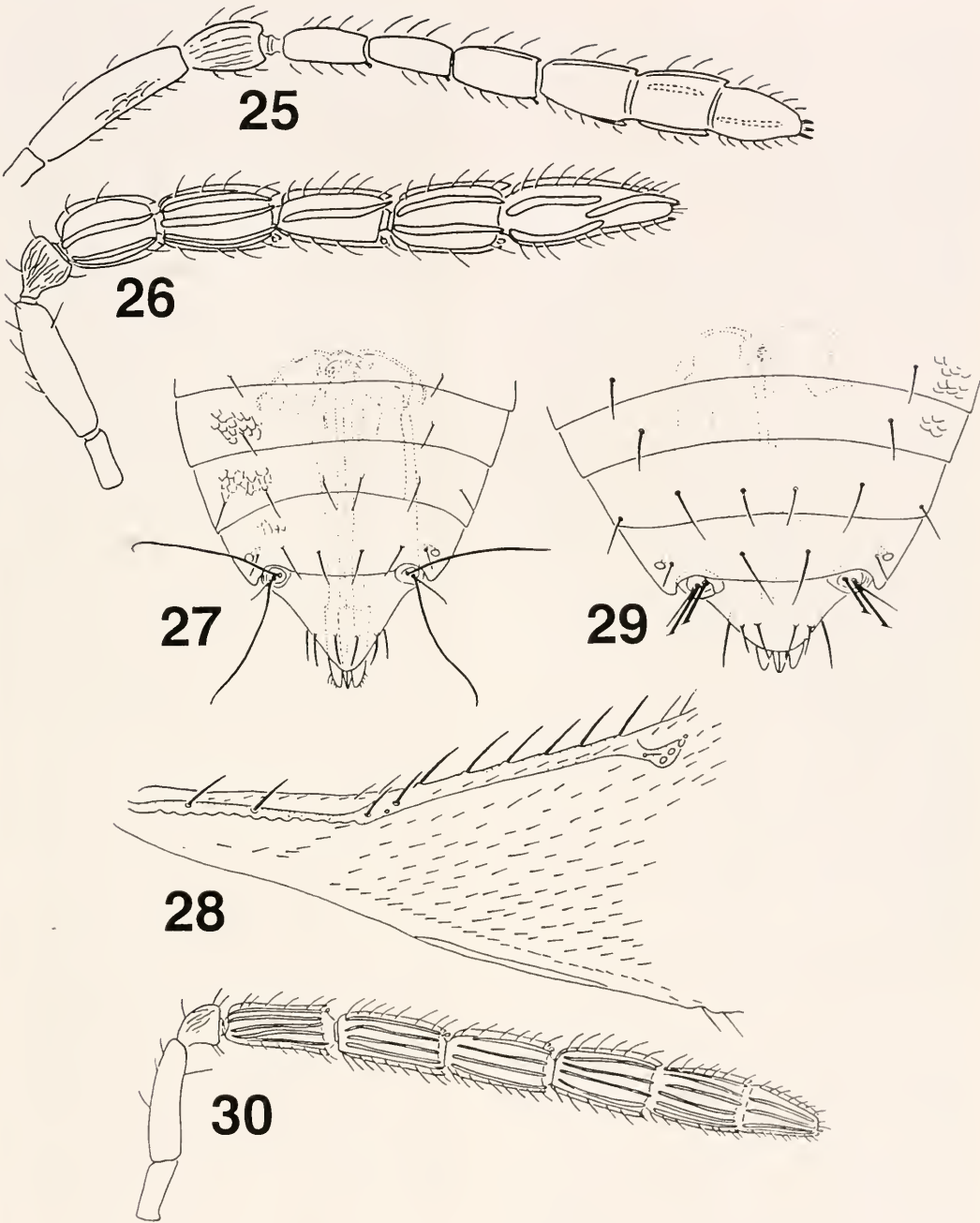
Encarsia protransvena; Schauff et al. 1996: 27. Described: female. Illust.; Huang & Polaszek 1998: 1941; Polaszek et al. 1999: 158.

Female.—Antenna with 6 flagellomeres, clava 3-segmented; F1 2.1–3.2× as long as broad and 0.7–1.1× as long as F3; antenna and entire body yellow except small spots of brown along inner margins of ocelli. Vertex weakly areolate, ocellar triangle areolate; dorsal setae stout. Maxillary palpus 1-segmented. Mandibles 3/3 dentate, teeth sharp or blunt. Mesosoma with weak

hexagonally areolate sculpture dorsally; midlobe usually with 4 pairs of setae (rarely with as few as 3 setae per side and as many as 5 pairs total), posterior and lateral setae much stouter than medial setae (almost twice as broad), side lobe with 3 pairs, axilla with 2 pairs (lateral pair minute), and scutellum 2 pairs, medial pair lateral to sensillae. Scutellar sensillae ovoid and separated by less than their own maximum diameter (rarely by a full diameter); median groove distinct. Apical spur of mid tibia 0.8–0.9× as long as basitarsus; basitarsomere of midtarsus with 2–3 strong pegs, tarsomeres 3–5 each with 1 apical peg. Tarsal formula 5-5-5. Fore wing 2.62–3.11× as long as broad, marginal fringe 0.20–0.40× width of fore wing; disc uniformly setose; costal cell with row of 12–18 small setae and 1–3 long marginal setae apically; submarginal vein with 2 large setae, basal area with 7–9 setae posterior to submarginal vein; frenal fold with several minute thornlike spines; wing hyaline. Metasoma laterally with weak cellulate reticulation; dorsal setal formula from tergite III: 2-2-2-6-6-6. Ovipositor 1.29–1.74× as long as mid tibia, 2.0–3.37× as long as clava, 0.6–0.7× as long as metasoma (base to tip of third valvula); third valvula stout (Fig. 15), 1.7–2.8× as long as broad, barely, if at all, extruded beyond epigynum, entirely yellow.

Male.—Overall coloration pale brown, darker brown pattern on head and mesosoma similar to *E. bimaculata* female, gaster entirely brown. Setation pattern of mesosoma and metasoma as in female, but difference in size of setae on midlobe of mesoscutum much less. Costal cell with 9–10 small setae and basal area with 5–7 setae. Basitarsomere of middle leg with only 2 pegs. Antenna with 5 flagellomeres, apical two flagellomeres (5&6) fused with linearia overlapping (Fig. 26).

Comments.—This species can be separated from other members of the *strenua* group by the shorter ovipositor and third valvulae, more delicate antenna (clava



Figs. 25–30. 25–28, *Encarsia protransvena*: 25, antenna of female; 26, antenna of male; 27, apex of gaster, dorsal view; 28, base of fore wing. 29, *Encarsia sophia*, apex of gaster. 30, *Encarsia strenua*, antenna of male.

only slightly broader than the funicle), and longer fore wing. The setae of the midlobe of the mesosoma are usually arranged in 4 pairs (rarely 3 or 5), whereas

they are almost always arranged in 5 pairs in *E. citri*, and the arrangement of setae (shorter and more apical) on the third valvulae is distinct from *E. citri*. Of the hun-

dreds of specimens examined, only the two males, collected at the same locality as other *E. protransvena* females, can be attributed to this species. This is probably the parasite recorded as *Encarsia strenua* attacking *Bemisia argentifolia* in South Carolina (Simmons 1998).

The specimens of *E. protransvena* described from China (1 female) and Taiwan (2 females) by Huang & Polaszek (1998) are nearly identical to those described in this paper. However, the taiwanese specimens have a band of 14 setae in the basal area of the fore wing (their fig. 273) as compared to a single row of only 7–9 setae in both *E. protransvena* and *E. citri*. They also describe 5 pairs of setae on the mid-lobe of the mesosoma, which is rarely encountered in specimens from the New World (usually 4 pairs). The chinese specimen agrees for all characters with *E. protransvena*, but it has a strongly and densely reticulate vertex, as compared to the very weak and more broadly spaced sculpture of all other *E. protransvena* examined, and the basal segment of the clava is more distinctly separated from the following segment. More material will need to be examined before these can be included or excluded from *E. protransvena* with confidence.

Hosts.—**Aleyrodidae:** *Aleurotrachelus rubi* Takahashi (Huang & Polaszek 1998), *Bemisia argentifolia* Bellows & Perring, *Bemisia tabaci* (Gennadius), *Dialeurodes citri* (Ashmead), *Dialeurodes citrifolii* (Morgan), *Dialeurodes kirkaldii* (Kotinsky) (Viggiani 1985a), *Parabemisia myricae* (Kuwana), *Trialeurodes abutiloneus* (Haldeman), *Trialeurodes packardii* (Morrill) (Huang & Polaszek 1998), *Trialeurodes variabilis* (Quaintance). **Diaspididae:** *Aspidiotus* sp.?, *Parlatoria ziziphi*?. [diaspidid hosts almost certainly are incorrect associations]

Distribution.—**Nearctic:** United States of America: California (Polaszek *et al.* 1992), Florida (Viggiani 1985a), Hawaii (Nguyen & Hamon 1989 [not examined]). **Neotropical:** Colombia; Cayman Islands; Hondu-

ras (Polaszek *et al.* 1992); Puerto Rico (Polaszek *et al.* 1992). **Palearctic:** Spain; Egypt (Polaszek *et al.* 1999). **Oriental:** People's Republic of China: Guangdong; Taiwan (Huang & Polaszek 1998).

Material Examined (390 females, 2 males). **Colombia:** Valle: Dagua, 28.v.1991, R. Caballero, 108, *Dialeurodes citrifolii* on *Citrus aurantifolia* (4♀ USNM). **Grand Cayman:** Cayman, 13.vi.1986, F.D. Bennett, Y729, whitefly on *Citrus* (1♀ USNM); Savannah, 17.x.1987, F.D. Bennett, 164, *Dialeurodes citrifolii* on *Citrus* (2♀ USNM). **Puerto Rico:** Rio Piedras, 5.v.1990, 4.vi.1990, 18.ix.1988, 18.xi.1988, 24.xi.1988,, F.D. Bennett, Y501, Y560, Y1042, Y1043, Y1051, 128, 828, 1585, *Dialeurodes citrifolii* on *Citrus*, *Dialeurodes citri* on *Citrus*, *Dialeurodes kirkaldii* on *Jasminum*, *Gynaspis* on *bromeliad* (15♀ USNM); Corozal, 27.xi.1988, 1.xii.1989, F.D. Bennett, 159, 161, *Dialeurodes citrifolii* on *Citrus* (5♀ USNM); Adjuntas, 15.xi.1988, F.D. Bennett, Y719, Y1045, Y1046, 163, *Dialeurodes citrifolii* on *Citrus* (8♀ USNM); Mayaguez, 16.xi.1988, F.D. Bennett, Y1047, 160, *Dialeurodes citrifolii* on *Citrus*, *Parlatoria ziziphi* on *Citrus* (5♀ USNM); Fortuna, 3.xii.1987, F.D. Bennett, 151, *Dialeurodes* on *Citrus* (8♀ USNM). **Spain:** Valencia, xi.1994, F.S. Mari, *Parabemisia myricae* (4♀ USNM). **USA: Florida:** Dade County: North Miami "Little Haiti", 28.v.1987, 22.vi.1987, R. Prange & F.D. Bennett, RP-1, *Dialeurodes citrifolii* on *Citrus* (20♀ 1♂ TAMU); 17.x.1987, F.D. Bennett & H. Glenn, FDB-3, *Dialeurodes citrifolii* on *Citrus*, *Dialeurodes citrifolii* on *Dioscorea alata* (10♀ TAMU); 19.i.1986, F.D. Bennett, J.H. Frank & R. Nguyen, *Dialeurodes citrifolii* on *Citrus* (1♀ USNM); 12.x.1987, F.D. Bennett, 1331, *Aspidiotus destructor* on *Dioscorea alata*, *Dialeurodes citrifolii* on *Dioscorea alata* (3♀ USNM); Miami, 12.x.1987, F.D. Bennett & H. Glenn, 87, *Dialeurodes citrifolii* on *Dioscorea alata* (6♀ 1♂ USNM); 29.x.1990, F.D. Bennett, 746, *Bemisia tabaci* on *Ricinus communis* (1♀ USNM). Alachua County: Gainesville, records for every month of the year, 1989 to 1993, collectors include F.D. Bennett, G.A. Evans, J. Marengo and L. Nong, host records include *Bemisia tabaci* on soybean, *Bemisia tabaci* on *Emilia sonchifolia*, *Trialeurodes abutilonea* on *Hibiscus mutabilis*, *Trialeurodes packardii* on *Cercis canadensis*, *Dialeurodes citri* on *Ligustrum sinense*, *Dialeurodes citri* on *Viburnum*, *Dialeurodes citrifolii* on *Citrus*, *Bemisia tabaci* on *Sesamum indicum*, *Bemisia tabaci* on *Chamaesyce hyssopifolia*, *Bemisia tabaci* on *Cassia obtusifolia*, *Bemisia tabaci* on *Euphorbia heterophylla*, *Bemisia tabaci* on *Brassica oleracea* var. *acephala*, *Bemisia tabaci* on *Hibiscus mutabilis*, *Bemisia tabaci* on *Desmodium tortuosum* (170♀ USNM); Micanopy, 3.iv.1988, 28.vii.1991, 11.ix.1988, 21.ix.1989, 21.x.1989, F.D. Bennett, Y287, 1, 95, 127, 154, 771, *Dialeurodes citri* on *Citrus*, *Dialeurodes citri* on *Viburnum*, *Dialeurodes citri* on *Melia azadarach*, *Trialeurodes packardii* on *Cercis canadensis* (18♀ USNM); Alachua,

xi.1992, H. McAuslane, 1339, *Bemisia tabaci* on peanut (3♀ USNM); near Alachua, 12.ix.1991, F.D. Bennett, Y399, Y400, *Bemisia tabaci* on soybean 5♀ (USNM). Monroe County: Isla Morada, 1.v.1993, F.D. Bennett, Y1060, *Dialeurodes citrifolii* on *Citrus aurantifolia* (3♀ USNM). Broward County: Pompano Beach, 22.iii.1992, 23.vii.1991, 23.viii.1991, 4.xi.1988, F.D. Bennett, Y274, Y437, Y490, Y664, *Bemisia tabaci* on *Emilia sonchifolia*, *Dialeurodes citrifolii* on *Citrus*, *Dialeurodes kirkaldyi* on *Jasminum* (10♀ USNM). Orange County: Apopka, 29.xi.1989, K. Hoelmer, 380, *Trialeurodes variabilis* on *Carica papaya* (2♀ USNM). Indian River County: Beach, 10.iv.1987, D. Mooney, *Crenidorsum* new species on *Coccoloba uvifera* (2♀ USNM). Jackson County: Mariana, 18.viii.1987, F.D. Bennett, 946, *Dialeurodes citri* on *Melia* (25♀ USNM). Bradford County: Starke, 26.iv.1989, W.A.A. Klerks, *Pseudaulacaspis cockerelli* (1♀ USNM). Gadsden County: Quincy IFAS, 13.ix.1991, F.D. Bennett, Y396, Y401, *Bemisia tabaci* on soybean, *Bemisia tabaci* on tomato (4♀ USNM). Palm Beach County: West Palm Beach, 6.ii.1991, 1.iv.1991, 13.vi.1992, 19.x.1991, F.D. Bennett, F104, Y428, Y450, Y838, 1183, *Dialeurodes kirkaldyi* on *Jasminum*, *Bemisia tabaci* on *Chamaesyce hyssopifolia*, *Bemisia tabaci* on *Emilia sonchifolia* (8♀ USNM). Hillsborough County: Ruskin, 29.vi.1990, *Eclipta* (1♀ USNM). Osceola County: Orange Creek, 18.iii.1990, F.D. Bennett, 407, *Trialeurodes abutilonea* on *Solanum americanum* (1♀ USNM); Canoe Creek, 22.xi.1990, F.D. Bennett, 1091, *Dialeurodes* or *Aleurothrixus floccosus* on *Citrus* (1♀ USNM). County?: Brywood, 4.vi.1992, F.D. Bennett, Y901, black whitefly on *Liquidambar styraciflua* (1♀ USNM). **South Carolina:** Charleston County: Charleston, 31.viii.1993, 7.ix.1993, 29.ix.1993, A. Simmons, 1610, 1614, 1615, *Bemisia tabaci* on sweetpotato (2♀ USNM). **Mississippi:** Simpson County: Magee, 10.ix.1994, D.H. Headrick, DHH96-0423, DHH96-0424, DHH96-0438, *Bemisia argentifolii* on *Cleome hasslerana* (3♀ UCRC). Forrest County: Hattiesburg, 5.ix.1994, D.H. Headrick, DHH94-0361, *Bemisia argentifolii* on okra (1♀ UCRC). **Georgia:** Bryan County: Savannah, 15.xi.1991, F.D. Bennett, 1161, *Bemisia tabaci* on *Chamaesyce hyssopifolia* (6♀ USNM). Tift County: Tifton, 20.x.1992, J. Chamberlain, 1355, 1395, *Bemisia tabaci* on *Gossypium hirsutum* (11♀ USNM); 29.iv.1992, 15.ix.1992, W. Hudson, Y714, Y715, Y716, Y717, 1346, *Bemisia tabaci* on *Gossypium hirsutum*, *Dialeurodes citri* on *Jasminum* (21♀ USNM).

***Encarsia sophia* (Girault & Dodd)**
(Fig. 28)

Coccophagus sophia Girault & Dodd, 1915: 49, 56. Type data: Australia: QLD, Cairns. Syntypes, female. Type depository: Brisbane: Queensland Museum, Queensland, Australia; type no. Hy.2926.

Prospaltella transvena Timberlake, 1926: 312–315. Type data: USA: Hawaii, Oahu. Holotype female. Type depository: Honolulu: Bernice P. Bishop Museum, Dept. Ent. Coll., HI, USA; type no. 5690. Described: both sexes. Illust. Reared from *Trialeurodes* [as *Aleyrodes*] *vaporariorum* on tomato. Placed in *lahorensis* group by Hayat (1989) and in *strenua* group by Polaszek *et al.* (1992) and Hayat (1998). Gerling (1985) states that *E. sublutea* is known in Hawaii as *E. transvena*. **New Synonymy.**

Prospaltella sophia; Compere 1931: 11. Change of combination.

Prospaltella sublutea Silvestri, 1931: 20–22. Type data: Somalia: Duca [?]. Syntypes, female. Type depository: IEUN. Described: female. Illust. Synonymy with *transvena* by Gerling & Rivnay in Viggiani 1985: 90.

Prospaltella bemisiae Ishii, 1938: 30. Type data: Japan: Ikawa-cho, Mei-Ken. Syntypes, female. Type depository: National Institute of Agroenvironmental Sciences, Tsukuba, Japan. Described: female. Synonymy with *transvena* by Polaszek *et al.* 1992: 388–389. Reared from *Parabemisia* [as *Bemisia*] *myricae* Kuwana.

Prospaltella flava Shafee, 1973: 254–255. Type data: India: Uttar Pradesh, Aligarh. Holotype female, by original designation. Type depository: Aligarh: Aligarh Muslim University, Department of Zoology, India. Described: female. Illust. Synonymy by Hayat 1989: 72. Preoccupied by *flavus* Compere 1936: 300. Questionably treated as a junior synonym of *transvena* by Viggiani (1985). The type material was reared from a coccid which, if correct, represents a significant departure in host range.

Encarsia sophia; Viggiani 1985b: 249. Described: female. Illust. Change of combination.

Encarsia transvena; Gerling & Rivnay in Viggiani 1985a: 90–92. Described: both sexes. Illust. Change of combination.

Encarsia shafeei Hayat, 1986: 163. Replacement name for *E. flava* Shafee.

Encarsia transvena; Hayat 1989: 71–73; Polaszek *et al.* 1992: 388–389; Schauff *et al.* 1996: 31–33; Hayat 1998: 205–207; Huang & Polaszek 1998: 1954–1956. Described: both sexes. Illust.

Comments.—This is the most distinctive species in the *strenua* group and can be recognized by the transversely striate ocellar triangle, a patch of longer setae in the

posterior half of the wing disc, and presence of only 4 setae on Mt7 (Polaszek *et al.* 1992; Schauff *et al.* 1997). All of the female specimens examined were completely yellow except for a single female from Thailand (ex *Bemisia tabaci* on *Lantana camara* [USNM]), which has the same dark pattern of colour as *E. bimaculata*.

The type specimen of *E. sophia*, like most of the Girault material, is in poor condition; however, all of the diagnostic features shared with *E. transvena*, and other species names currently synonymized with *E. transvena*, are clearly visible. Since it was described as different species in Australia (Girault & Dodd 1915), Hawaii (Timberlake 1926), Somalia (Silvestri 1931), and Japan (1938), we assume that this group was widespread in the Old World, prior to recent movements of species for use in the biological control of whiteflies. Both authors of this paper have examined several hundred *E. transvena* from around the world and found no diagnostic characters that would separate any population as distinct from the others. Recent studies, however, have shown mating incompatibilities and morphometric (shape) differences between populations of *E. transvena* from Spain and Pakistan (G. Viggiani, pers. comm.) that allude to the potential for this to be a cryptic or sibling species complex. Should we proceed with the synonymy or wait for further evidence of potential species boundary characteristics? The synonymy is justified on both philosophical and practical grounds. For practical purposes, the assignment of an appropriate specific epithet to any of the geographically isolated populations is complicated by their taxonomic history. Five names were proposed within this complex, of which *E. sophia* is the oldest, and *E. transvena* (described from Hawaii, where it may have been accidentally introduced from Japan, south-east Asia or Australia) is probably the least applicable to the populations from Pakistan or Spain under study. If there has

been some accidental movement, especially to Hawaii (type locality of *E. transvena*), determining the origin and movements through introductions of each geographical population will be essential to the correct assignment of names, if this is indeed a species complex.

Especially for the purposes of biological control and the associated need for accurate identification of museum and field material, what concept of a species is most useful? Among the many definitions proposed, there are only two basic and, in some ways opposable, concepts. The Biological Species Concept (Mayr 1963) requires that populations of the same species, whether they are in contact or not, have the potential to interbreed. The degree and conditions under which interbreeding will take place are problematic (Donoghue 1985), especially when they are used to assess allopatric populations that have varying degrees of reproductive incompatibility (cf. Rosen & DeBach 1979). The ability to interbreed in Aphelinidae and other Chalcidoidea can be further complicated by other factors, such as endosymbiotic bacteria that can induce reproductive incompatibility within or between populations (O'Neill *et al.* 1997; Luck *et al.* in press). These incompatible populations can even be cured through antibiotics or heat treatments and interbreeding reestablished (Stouthamer & Luck 1993; Luck *et al.* in press), which brings into question the criterion of incompatibility for separating otherwise indistinguishable populations that have been treated previously as either cryptic, sibling or semi species. In contrast, under a Phylogenetic Species Concept (Donoghue 1985), at least one diagnostic character is required for each species to denote an evolutionary lineage. The simple notion of reproductive incompatibility, the foundation of the Biological Species Concept, is not sufficient. A discrete morphological character found in all individuals is usually taken as the best criterion for

separating species; species are both diagnosable and unique. Whether both molecular and morphometric (shape) characteristics are considered diagnostic under a Phylogenetic Species Concept is debatable, especially since they may be describing only population level differences that do not contribute to the "potential" for a species to interbreed (Avise & Wollenberg 1997). In any case, differences must be demonstrated over the range of a species to assure that they are not merely representative of clinal variation in a series of populations belonging to a single species. Currently, *E. sophia* and *E. transvena*, and all of the names synonymized of *E. transvena*, cannot be distinguished using diagnostic morphological characters, and synonymy under the oldest valid senior name, *E. sophia*, is justified.

Hosts.—**Aleyrodidae:** *Acaudaleyrododes rhachipora* (Singh) (Hayat 1989), *Aleurocybotus indicus* David & Subramaniam (Polaszek *et al.* 1992), *Aleurodicus dispersus* Russell (Polaszek *et al.* 1992), *Aleurolobus* sp. near *niloticus* (Hayat 1989a), *Bemisia*? (= *Aleyrododes*) *hibisci* (USNM 29067), *Bemisia tabaci* (Gennadius) (Polaszek *et al.* 1992, Hayat 1989, Gerling 1985), *Parabemisia myricae* (Kuwana) (Polaszek *et al.* 1992), *Pealius hibisci* (Kotinsky) (Timberlake 1926), *Trialeurodes ricini* (Misra) (Hayat 1998), *Trialeurodes vaporariorum* Westwood (Polaszek *et al.* 1992, Timberlake 1926, Gerling 1985). **Aphididae:** *Aphis sacchari* Zehntner? (Timberlake 1926). **Coccidae:**? (Shafee 1973). **Psyllidae:** *Diaphorina citri* Kuwayama (Polaszek *et al.* 1992). [The psyllid host is correct, although possibly *E. sophia* is a hyperparasitoid on *Tamarixia radiata* (Waterston) [Huang & Polaszek 1998], so the aphid and coccid associations also may be "primary" hosts of hyperparasitic males.]

Distribution.—Cosmopolitan in the Old World, introduced in the New World. **Afrotropical:** Burundi; Cape Verde (Hayat 1998); Ivory Coast; Morocco; Niger (Hayat 1998); Sierra Leone; Somalia (Silvestri

1931). **Oriental:** Hawaiian Islands (Timberlake 1926); Hong Kong; India (Hayat 1989); Indonesia; Sri Lanka (Hayat 1998); Pakistan (Hayat 1989); People's Republic of China (Huang & Polaszek 1998); Taiwan; Thailand. **Palaeartic:** Japan (Ishii 1938); Spain.

Material Examined (289 females, 71 males).—**Burundi:** Bujumbura, vii.1987, J. Yaninek, whitefly on *Cassava* (1♀ USNM). **Hong Kong:** Kowloon Park, 14.vii.1992, F.D. Bennett, Y944, *Bemisia tabaci* on *Chamaesyce* (?) *hirta* (1♀ USNM). **India:** Rajkot, 9.ii.1958, G.W. Angolet, whitefly on *Ricinus communis* (4♀ USNM); India (no other locality), 19.xii.1990, G. Butler, *Bemisia tabaci* (1♀ USNM). **Indonesia:** Java: Bandoeng, x.1929, C. P. Clausen, 2420, *Asterochiton* (10♀ UCRC). **Ivory Coast:** 20 km west of Abidjan, 21.iv.1988, L.D.C. Fishppol, 125, *Bemisia tabaci* on *Manihot esculentum* (2♀ USNM). **Japan:** Shikoku: Kochi, 23.vii.1980, P. DeBach, R.80.28, R.80.29, R.80.34, *Parabemisia myricae* on *Morus*, *Parabemisia myricae* on *Citrus* (43♀ 1♂ UCRC); 20–25.ix.1979, M. Rose, R79-67-1 & 2, *Parabemisia myricae* on *Morus* (13♀ 5♂ UCRC); Kyushu: Kagoshima City, 8.viii.1972, S. Ogo, R72-42, *Dialeurodes citri* on *Citrus* (3♀ UCRC); Honshu: Mie Prefecture, near Kuana City, 11, 15, 16, 18, 20, 21.viii.1981, M. Rose, R81-34, R81-35, R81-36, R81-37, R81-39, R81-40, R81-41, R81-42, *Parabemisia myricae* on *Morus* (60♀ 4♂ UCRC); Shizuoka, 17.vii.1981, 5.viii.1982, K. Furuhashi, R82-30, on *Morus* (4♀ UCRC); 22–24.viii.1981, M. Rose, R81-43, *Parabemisia myricae* on *Morus* (1♀ UCRC). **Morocco:** Agadir, vi.1992, *Parabemisia myricae* (1♀ USNM). **Niger:** 4.xi.1987, Hansen, CIE A19340, *Aleurocybotus indicus* on rice (1♀ USNM). **Pakistan:** Sialkot, 25.ix.1969, R. Ahmad, R69-110, *Dialeurodes citri* on *Citrus* (1♂ UCRC); Pakistan (no other locality), 15.v.1987, L. Osborne, 803, *Bemisia tabaci* (1♀ USNM). **People's Republic of China:** Sichuan Province: Bei-Pei District, 19.viii.1980, P. DeBach, C3, whitefly on *Morus* (7♀ 1♂ UCRC); Guangdong Province, Guangzhou, 11.vii.1992, F.D. Bennett, Y894, whitefly on *Lactuca* (1♂ USNM). **Sierra Leone:** viii.1960, *Bemisia* (7♀ USNM). **Spain:** Murcia, 19.vii.1994, EBCL—A. Kirk & L. Lacey, M93002, *Bemisia tabaci* on *Lantana* (19♀ UCRC). **Taiwan:** Tao-yuan, 3.xii.1993, C. Moomaw, Mission Biological Control Lab culture (Texas) M93054, *Bemisia* on *Poinsettia* (3♀ TAMU). **Thailand:** Chiang Mai, 14.iii.1994, L. Lacey & A. Kirk, M94041, *Bemisia tabaci* on *Poinsettia* (9♀ UCRC, 1♀ 1♂ TAMU); Chiang Mai University, 15.i.1993, F.D. Bennett, Y1009, whitefly on *Hibiscus mutabilis* (1♀ USNM); Pang Hang, 15.iii.1994, L. Lacey & A. Kirk, M94049, *Bemisia tabaci* on *Xanthium*; Ban Ton Tea, 20.i.1992, F.D. Bennett, 1224, *Bemisia tabaci* on *Gossypium hirsutum* (6♀ USNM); near Bangkok, iii.1992, F.D. Bennett, 1245, *Bemisia tabaci* on *Solanum melon-*

gena (6♀ USNM). USA: **Arizona**: Cochise County: Guadalupe Canyon, 31 miles east of Douglas, 14.ix.1978, J.B. Woolley, 78035, whiteflies on mesquite (1♀ TAMU). **Florida**: Dade County: Miami, 14.vi.1992, 21.vii. 1991, 22.vii.1991, 31.viii.1991, 19.x.1991, F.D. Bennett, Y276, Y277, Y358, Y459, Y834, *Bemisia tabaci* on *Chamaesyce hyssopifolia*, *Bemisia tabaci* on *Euphorbia* (11♀ 19♂ USNM); Homestead, 4.v.1992, F.D. Bennett, Y757, *Bemisia tabaci* on *Emilia sonchifolia* (1♂ USNM); Snapper Creek, 13.vi.1992, 14.vi.1992, 19.x.1991, F.D. Bennett, Y457, Y830, Y837, *Bemisia tabaci* on *Emilia sonchifolia*, *Bemisia tabaci* on *Chamaesyce hyssopifolia* (4♀ 4♂ USNM). Alachua County: Alachua, xi.1992, H. McAuslane, 1376, *Bemisia* on peanut (3♀ USNM); Gainesville, 19.iii.1968, M. Kosztarab 874, *Diaspis* on *Opuntia* (2♀ USNM); 3.v.1992, G.A. Evans, 1251, on *Ilex* (1♂ USNM); 27.viii.1992, F.D. Bennett, Y936, *Bemisia tabaci* on *Sesamum indicum* (1♀ USNM); Micanopy, 20.i.1990, F.D. Bennett, Y487, whitefly on *Citrus* (1♀ USNM). Saint Lucie County: Fort Pierce, 9.viii.1992, F.D. Bennett, Y904, *Bemisia tabaci* on *Emilia sonchifolia* (2♀ 1♂ USNM). Okeechobee: Fort Drum, 17.x.1991, F.D. Bennett, Y440, *Bemisia tabaci* on *Emilia* (3♀ 6♂ USNM). Orange County: Apopka, 15.viii.1988, L. Osborne, *Bemisia tabaci* on *Euphorbia* (17♀ 4♂ TAMU); 10.ix.1987, Rose & Osborne, T87032, *Bemisia tabaci* (?) on *Euphorbia* (4♂ TAMU); vi-vii.1989, 14.x.1989, 25.x.1989, 29.xi.1989, K. Hoelmer, *Bemisia tabaci* on *Lantana*, *Trialeurodes variabilis* on papaya (1♀ 3♂ USNM). Broward County: Pompano Beach, 22.iii.1992, v.1993, 10.viii.1992, 19.x.1991, 19.xi.1991, F.D. Bennett, Y448, Y541, Y665, Y908, Y1056, *Bemisia tabaci* on *Chamaesyce hyssopifolia*, *Bemisia tabaci* on *Emilia sonchifolia* (13♀ 7♂ USNM). Palm Beach County: West Palm Beach, 11.iv.1992, 10.viii.1992, 11.ix.1992, F.D. Bennett, Y907, Y933, 1559, *Bemisia tabaci* on *Emilia sonchifolia*, *Bemisia tabaci* on *Chamaesyce hyssopifolia* (3♀ 4♂ USNM). Monroe County: Isla Morada, 30.iv.1993, 18.x.1991, F.D. Bennett, Y453, Y1108, *Bemisia tabaci* on *Chamaesyce hyssopifolia*, *Bemisia tabaci* on *Chamaesyce hirta* (2♀ 1♂ USNM); Key Largo, 18.x.1991, F.D. Bennett, Y444, *Bemisia tabaci* on *Desmodium tortuosum* (3♀ 3♂ USNM). Manatee County: Bradenton, 13.v.1993, E. Vasquez, Y1053, *Bemisia tabaci* (4♀ 2♂ USNM). Texas: Hidalgo County, Mission Biological Control Lab, 16.xii.1993, M93002 (MBCL culture voucher specimen), *Bemisia tabaci* (1♀ TAMU). **California**: Orange County: U.C. South Coast Field Station, 15–16.xii.1982, S. Key, *Parabemisia myricae* on lemon (9♀ 1♂ UCRC); Los Angeles County: San Gabriel, 22.iv.1982, Rose & Ferrentino, *Parabemisia myricae* on orange (1♀ UCRC). **Hawaii**: Oahu: Moiliili, 15.iii.1984, B. Kumashiro, *Bemisia tabaci* on eggplant (7♀ TAMU).

Encarsia strenua (Silvestri)
(Figs. 16, 30)

Prospaltella strenua Silvestri, 1928: 34–36. Type data: China: Macao. Holotype female, by

monotypy. Type depository: IEUN. Described: female. Illust. Reared from *Bemisia giffardii* on *Citrus*. Placed in *strenua* group by Viggiani & Mazzone (1979) and Hayat (1989).

Encarsia strenua, Viggiani & Mazzone, 1979: 46. Change of combination.

Encarsia strenua; Polaszek *et al.* 1992: 388; Schauff *et al.* 1996: 29. Described: female. Illust. Broadly defined to include what is now recognized as *E. protransvena* and *E. citri*.

Encarsia strenua; Polaszek & Huang 1998: 1951–53. Described: female. Illust. Based on Chinese and Taiwan material.

Female.—Antenna with 6 flagellomeres, clava 3-segmented; F1 2.6–3.6× as long as broad and 0.9–1.0× as long as F3; antenna yellow basally, darkened beyond or including pedicel. Vertex and ocellar triangle strongly areolate; head yellow except for weak infuscation on inner margins of ocelli; dorsal setae robust. Maxillary palpus 1-segmented. Mandibles 2/2 or 2/3 dentate, teeth blunt to hardly recognizable, dorsal tooth, if visible, minute. Mesosoma mostly yellow except pronotum pale brown medially and anterior margin of midlobe of mesoscutum sometimes pale brown, rarely axillae and metasoma more extensively pale brown. Mesosoma with hexagonally areolate sculpture dorsally; midlobe with 4–5 pairs of setae, posterior and lateral setae noticeably stouter than medial setae, side lobe with 3 pairs (rarely with additional seta), axilla with 2 pairs (lateral pair minute), and scutellum 2 pairs, medial pair lateral to sensillae. Scutellar sensillae ovoid and separated by less than their own maximum diameter; median groove narrow and distinct. Apical spur of mid tibia 0.7–0.9× as long as basitarsus; basitarsomere of midtarsus with 4–5 large pegs, tarsomeres 3–5 each with 1 robust apical peg, rarely a single peg on tarsomere 2. Tarsal formula 5–5–5. Fore wing 2.44–2.67× as long as broad, marginal fringe 0.13–0.29× width of fore wing; disc uniformly setose; costal cell with row of 13–23 small setae and 1–3

long marginal setae apically; submarginal vein with 2 large setae, basal area with 8–12 setae posterior to submarginal vein; frenal fold without spines; wing hyaline. Metasoma mostly yellow, tergites I + II sometimes with faint infuscation, usually yellow; laterally with weak cellulate reticulation; dorsal setal formula from tergite III: 2-2-2-6-6-6. Ovipositor $1.56\text{--}1.97\times$ as long as mid tibia, $2.43\text{--}3.26\times$ as long as clava, $0.8\text{--}0.9\times$ as long as metasoma (base to tip of third valvula); third valvula elongate, $2.9\text{--}4.7\times$ as long as broad, extruded beyond epygium, yellow except for extreme tip dark brown.

Male.—Overall coloration pale brown, darker brown pattern on head and mesosoma similar to *E. bimaculata* female, gaster entirely brown. Setation pattern of mesosoma and metasoma as in female but midlobe of mesoscutum with 4–5 pairs of setae. Midbasitarsomere with only 2 pegs. Antenna with 5 flagellomeres, apical two flagellomeres (5&6) fused, with segments distinguished only by a break in the pattern of linearia (Fig. 30).

Comments.—The Californian population differs from the Asian forms by having darkened axillae and gaster (yellow in Asian forms) and the third valvulae less elongate, being less than $3.5\times$ as long as broad. All females of *E. strenua* have at least 4 large pegs on the midbasitarsomere, a long ovipositor and third valvula, 8–12 setae in the basal area of the fore wing, and the tip of the third valvula brown. The males from India have a slightly more elongate antenna (ca. $1.2\times$ as long as head width), whereas the single male has a slightly more compact antenna (ca. $1.1\times$ as long as head width). The difference could be due to different mounting techniques, and for other characters the males were identical.

Hosts.—**Aleyrodidae:** *Aleurobus subrotundus* Silvestri (Clausen 1934), *Aleuroplatus* (Clausen 1934), *Asterochilton* (Clausen 1934), *Bemisia giffardii* (Kotinsky) (Silvestri 1928), *Dialeurodes citri* (Ashmead) (Polasz-

ek *et al.* 1992), *Dialeurodes kirkaldii* (Kotinsky) (Polaszek *et al.* 1992), *Parabemisia myricae* (Kuwana) and *Siphonius phyllireae* (Haliday). The host records from Clausen (1934) have not been verified. The host range presented here is more restricted than that of Polaszek *et al.* (1992) after exclusion of much of the New World material now placed as *E. protransvena*.

Distribution.—**Nearctic:** USA (California). **Oriental:** China (Fujian, Guangdong) (Huang & Polaszek 1998); Hong Kong (Polaszek *et al.* 1992); India; Macau (Silvestri 1928).

Material Examined (60 females, 40 males).—**Hong Kong:** Kowloon, 2.xii.1986, F. Bennett, ex Jasmine whitefly on *Jasminium* (1♀ 1♂ USNM, 1♀ BMNH). **India:** Uttar Pradesh: Ranikhet, 4.viii, 7.viii, 18–19.viii, 11.ix, 10.ix, 7.x.1969, G. Chamora, R69-81, R69-85, R69-89, R69-101, R69-103, *D. citri* on *Citrus* (8♀ 24♂ UCRC); West Bengal: Kalimpong, 2.ix, 12.ix, 18.ix.1969, Kurup (CIBC), R69-98, R69-104, 69-106, R69-116, *Dialeurodes citri* on *Citrus* (43♀ 21♂ UCRC); Kayala: Bakarkhola [locality not verified], 21.vii.1969, G. Chondra, R69-77 (3♀ UCRC); [locality?] R69-93 (37♂ UCRC). **P.R. China:** Guangdong: Guangzhou, 11.vii.1992, F. Bennett Y941, *Dialeurodes* on *Citrus* (1♀ USNM). **Israel?** [no locality, just Tel-Aviv University header]: viii.1990, D. Gerling, on leaf with *Siphonius phyllireae* (2♀ USNM).

ACKNOWLEDGMENTS

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A Peculiar New Genus and Species of Entedoninae (Chalcidoidea: Eulophidae) from Southeast Asia

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Abstract.—*Ambocybe petiolata* Ubaidillah and LaSalle gen. and sp. n. from Peninsular Malaysia, Sulawesi and Papua New Guinea is described and illustrated and placed in the Entedoninae (Hymenoptera: Eulophidae). In addition to having several unique features, *Ambocybe* lacks important characters that have been used previously as defining characters of the Entedoninae. Possible relationships of the new genus to other entedonine genera are discussed.

Sorting of mass-collected material from Southeast Asia revealed a peculiar genus of Entedoninae (Eulophidae). This genus differs from other entedonines in having a strong ridge surrounding the frons on the front of the head, and a similar one surrounding the entire occipital region on the back of the head. In addition, it differs from most entedonines in having several pairs of setae on the scutellum, having a single dorsal seta on the submarginal vein, and lacking a frontal sulcus.

We are describing this genus as part of an interest among the authors to, (1) describe the eulophid fauna of Southeast Asia, and (2) provide a necessary framework for understanding variation within the Eulophidae, including exceptions to characters used for subfamily definition.

A single diagnosis and description are offered for this new genus and new species. Without additional species it is impossible to distinguish between species level and genus level characters.

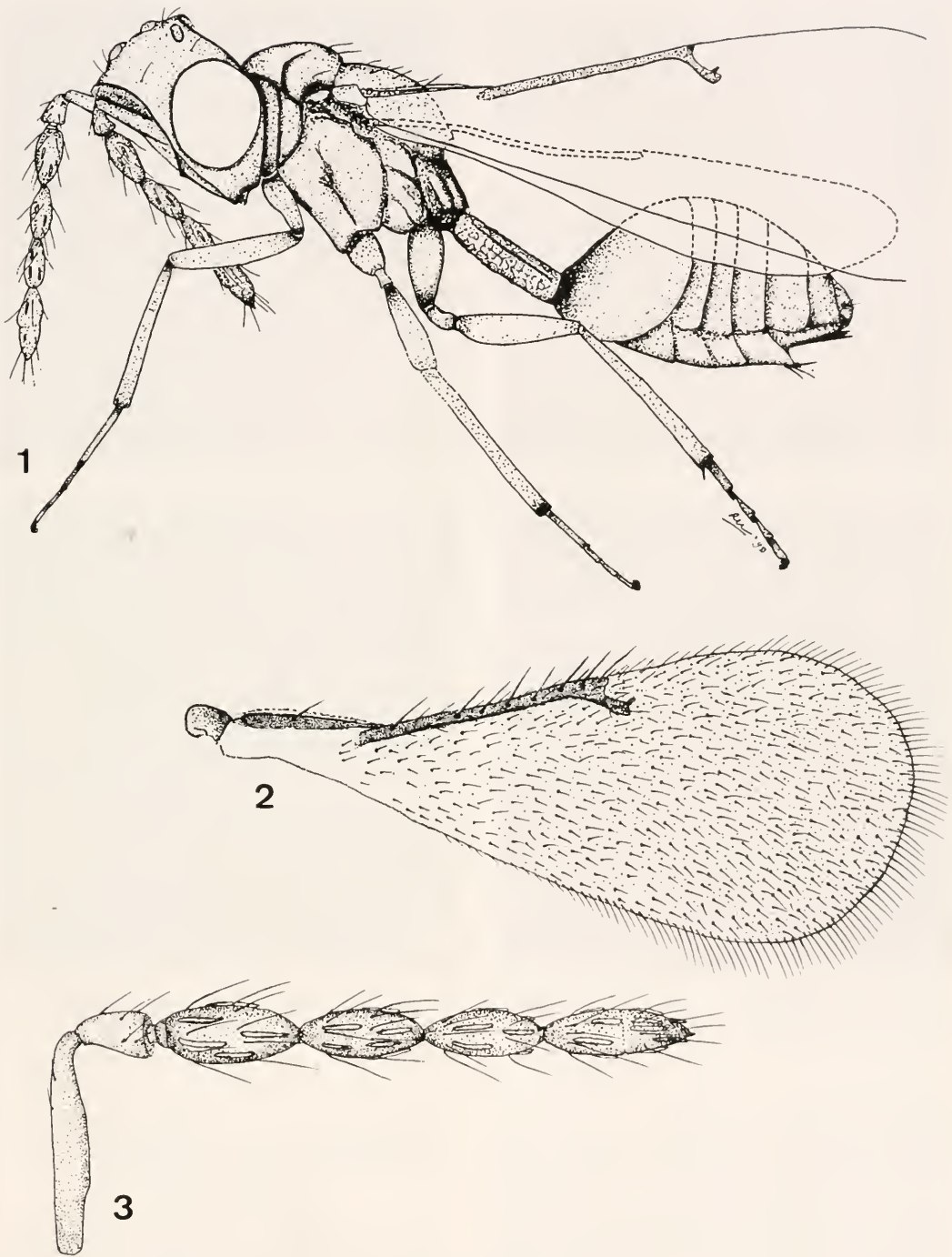
Acronyms used in the text are as follows. Collections: ANIC, Australian National Insect Collection, CSIRO, Canberra,

Australia; BMNH, The Natural History Museum, London, UK; MZB, Museum Zoologicum Bogoriense, Bogor, Indonesia; UCR, University of California, Riverside, California, USA; USNM, United States National Museum of Natural History, Washington, D.C., USA. Terminology: MV, marginal vein; OOL, oculo-ocular length, the distance between the lateral ocellus and eye margin; POL, postero-ocular length, the distance between the lateral ocelli; PMV, postmarginal vein; SMV, submarginal vein; and SV, stigmal vein.

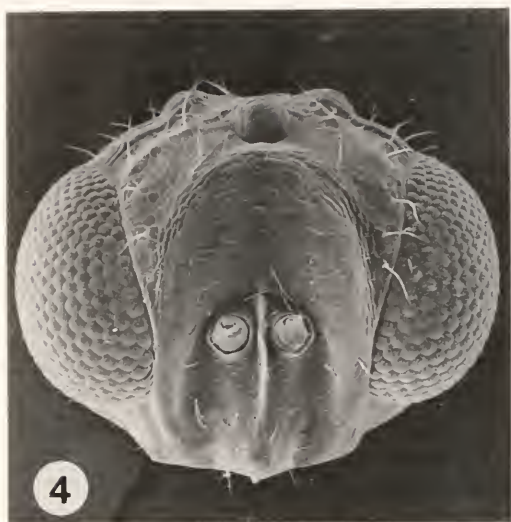
Ambocybe Ubaidillah and LaSalle, new genus (Figs. 1–7)

Type species: *Ambocybe petiolata* Ubaidillah and LaSalle

Diagnosis.—Head with a strong, inverted U-shaped ridge surrounding the frons (Fig. 4), and a similar one surrounding entire occipital region (Fig. 5). Scutellum with 5–6 pairs of setae (Fig. 6). Submarginal vein with single dorsal seta (Fig. 2). Forewing with speculum absent. Fore bas-



Figs. 1–3. *Ambocybe petiolata*, female. 1. Habitus. 2. Forewing. 3. Antenna.



Figs. 4-7. *Ambocybe petiolata*, female: 4. Head, frontal view. 5. Head and mesosoma. 6. Scutellum and propodeum. 7. Propodeum and petiole.

itarsus elongate, slender, about twice as long as second segment (Fig. 1). Pronotum small, not visible in dorsal view (Fig. 5). Propodeum with distinct plicae; with two subparallel median carinae; area between median carinae slightly depressed and sculptured; plicae converging along posterior margin of propodeum and ending at arcuate adpetiolar carinae (Fig. 6). Petiole long and slender, reticulate dorsally (Fig. 7).

Ambocybe petiolata Ubaidillah and
LaSalle, new species
(Figs. 1-7)

Female.—Length of body 1.0–1.3 mm; length of forewing 0.75–0.95 mm. Head and body dark brown, lower face and metasoma paler. Antenna yellow-brown. Legs pale yellow except coxae yellow-brown. Sculpture on mesosoma reticulate, shiny.

Head (Figs. 4, 5) broad with shiny, weak coriaceous to imbricate sculpture and inconspicuous pilosity. Compound eyes convex and large. Frons defined by an inverted U-shaped ridge extending from anterior ocellus along eye margin to lower face. Lower face produced medially, concealing clypeus, which is reduced and inflected. Strong longitudinal median carina present between toruli. Back of head with strong ridge forming a large curve from vertex to gena and defining a large, smooth occiput. Temple narrow. Vertex shiny, although finely wrinkled, with fine transverse carina between lateral ocellus and compound eyes. POL/OOL = 1.6. Antenna (Fig. 3) with scape long and slender, about 5 times as long as wide, reaching above vertex. Pedicel short, slender, about 2 times as long as wide. Two transverse anelli. Funicle with three segments, all longer than wide. Club with two segments.

Mesosoma (Figs. 5–6) except propodeum reticulate. Pronotum reduced and not visible in dorsal view. Mesoscutum transverse; midlobe with 2–3 pairs of setae; notaulus incomplete, but indicated posteriorly by wide shallow depression. Scutellum longer than broad, with 5–6 pairs of setae; slightly produced posteriorly so dorsellum concealed in dorsal view. Propodeum medially 0.40–0.50 as long as length of scutellum, with plicae and paired, subparallel median carinae; median carinae and plicae joined by transverse carina at posterior margin of scutellum. Legs long and slender; fore basitarsus elongate, slender, about twice as long as second segment (Fig. 1). Forewing (Fig. 2) with SMV tapering at apex and joining parastigma anteriorly to base of parastigma. Speculum absent. SMV with 1 dorsal seta. PMV very reduced, almost absent. MV/SMV 1.5–1.75; MV/SV 4.45–5.4.

Metasoma. Petiole (Fig. 7) unusually long, about three times as long as wide; broader distally; with 2 setae on each lateral margin; reticulate dorsally, with lon-

gitudinal dorso-lateral carina. Gaster smooth, elongate elliptical. Ovipositor short, apex not visible in dorsal view. Hypopygium extending 0.75–0.90 length of gaster.

Male.—Unknown.

Biology and host.—Unknown.

Distribution.—Currently known from Peninsular Malaysia, Sulawesi (Indonesia) and Papua New Guinea. The somewhat disjunct distribution spans both sides of Wallace Line, and suggests that this species may be more widespread through Southeast Asia and Australasia.

Material examined.—Holotype female: **INDONESIA**, Sulawesi, Dumoga Bone N.P., Toraut, 16–23.v.1985, Malaise trap, J.S. Noyes (MZB) (card mounted). 21 female paratypes (all card mounted): **INDONESIA**: same data as holotype (5 females MZB; 5 females BMNH; 3 females USNM; 3 females ANIC); same data as holotype but v.1985 (2 females BMNH). **MALAYSIA**, Selangor, Serdang, UPM Campus, 25.viii–3.ix.1992, Malaise Trap, J. LaSalle (1 female BMNH). **PAPUA NEW GUINEA**: Central Province, ~45 km NW Port Moresby, 5km NW Brown River Bridge (Hiritano Hwy).29.xii.1985, G. Gordh, rainforest (1 female UCR); Central Province, 20 km SE Port Moresby, 1.i.1986, G. Gordh, forest edge (1 female UCR).

Etymology.—*Ambocybe* is formed from the Greek *ambon*, for ridge or crest, and *kybe* for head. Gender feminine. The specific name, *petiolata*, reflects the presence of a long petiole.

Discussion.—*Ambocybe* is placed in the Entedoninae, although it differs from most other entedonines in several important characters. The Entedoninae is one of the best defined subfamilies of the Eulophidae (Bouček 1988, Schauff 1991). It is easily recognised by a variety of characters which include: scutellum with a single pair of setae (as opposed to two or more pairs); submarginal vein with two dorsal setae; mesoscutal midlobe with two pairs of setae; male scape with sensory pores re-

stricted to the ventral edge; face with frontal sulcus distinctly separated from the anterior ocellus; propodeum with subspiracular tubercles; marginal vein relatively long; stigmal vein relatively short (Bouček 1988, Schauff 1991). The most important of these characters are the single pair of setae on the scutellum, the presence of only two strong setae on the submarginal vein, and the position of the frontal sulcus. None of these characters are present in *Ambocybe*, however all of these characters do show variation within the Entedoninae.

A single pair of scutellar setae is one of the best characters for defining the Entedoninae (Schauff 1991), and is found in almost all members of the subfamily. *Ambocybe* has 5–6 pairs of setae on the scutellum. There are a few other entedonines which have more than a single pair of setae on the scutellum. These include *Parahorismenus* Girault (Bouček 1988), two species of *Pediobius* Walker (Kerrich 1973, Bouček 1977), and all members of the *Entedononecremnus* genus group in the Euderomphalini (*Entedononecremnus* Girault, *Aleuroctonus* LaSalle and Schauff, *Dasyomphale* LaSalle and Schauff; see LaSalle and Schauff 1994).

Another important character for defining the Entedoninae is the submarginal vein with two usually strong dorsal setae (Schauff 1991). *Ambocybe* only has a single seta. This character is also known in *Myrmokata* Bouček (Bouček 1972) and two genera in the Euderomphalini, *Pomphale* Husain, Rauf and Kudeshia and *Baeocntedon* Girault (LaSalle and Schauff 1994).

The frontal sulcus in Entedoninae is generally distinctly separated from the anterior ocellus (Schauff 1991). This sulcus is absent in *Ambocybe*. The frontal sulcus is absent from several other Entedoninae, including many species of *Entedon* Dalman and some *Paracrias* Ashmead (Schauff 1991), as well as members of the *Entedononecremnus* genus group (see above).

The mesoscutal midlobe in Entedoninae typically has two pairs of setae (Schauff

1991), but this character is more homoplastic than the preceding three characters, and there are numerous exceptions. *Ambocybe* has 2–3 pairs of setae on the mesoscutal midlobe.

Despite the numerous characters by which *Ambocybe* differs from other Entedoninae, we still feel that it is best placed in this subfamily. Characters to support this are the incomplete notauli, the structure of the carinae and plicae on the propodeum which are similar to those in *Pediobius* Walker, the presence of a small subspiracular propodeal tubercle, the relatively long marginal vein, and the short stigmal vein.

The relationships of *Ambocybe* remain unknown. The presence of distinct plicae on the propodeum would suggest an affiliation with other genera which also have this putatively synapomorphic character (such as *Pediobius* Walker, *Pediobomyia* Girault, *Rhynchentedon* Girault, *Apleurotropis* Girault, *Pleurotroppopsis* Girault, *Parahorismenus* Girault, *Zaommomentedon* Girault, *Schizocharis* Kerrich, *Platocharis* Kerrich, *Kratoysma* Bouček, *Horismenus* Walker, *Paracrias* Ashmead). Within this group of genera, it could be closest to those genera which possess some form of paired median carinae on the propodeum, such as *Pediobius*, *Pediobomyia*, and *Rhynchentedon*. However, it is not at all clear that *Ambocybe* is related to these genera, because all of the above genera possess a distinct transverse carina on the pronotum, and the pronotum is distinct and clearly visible in dorsal view. *Ambocybe* lacks a transverse carina on the pronotum, and the pronotum is short and not visible in dorsal view.

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An Introduced Species of *Epichrysocharis* (Hymenoptera: Eulophidae) Producing Galls on *Eucalyptus* in California with Notes on the Described Species and Placement of the Genus

M. E. SCHAUFF AND R. GARRISON

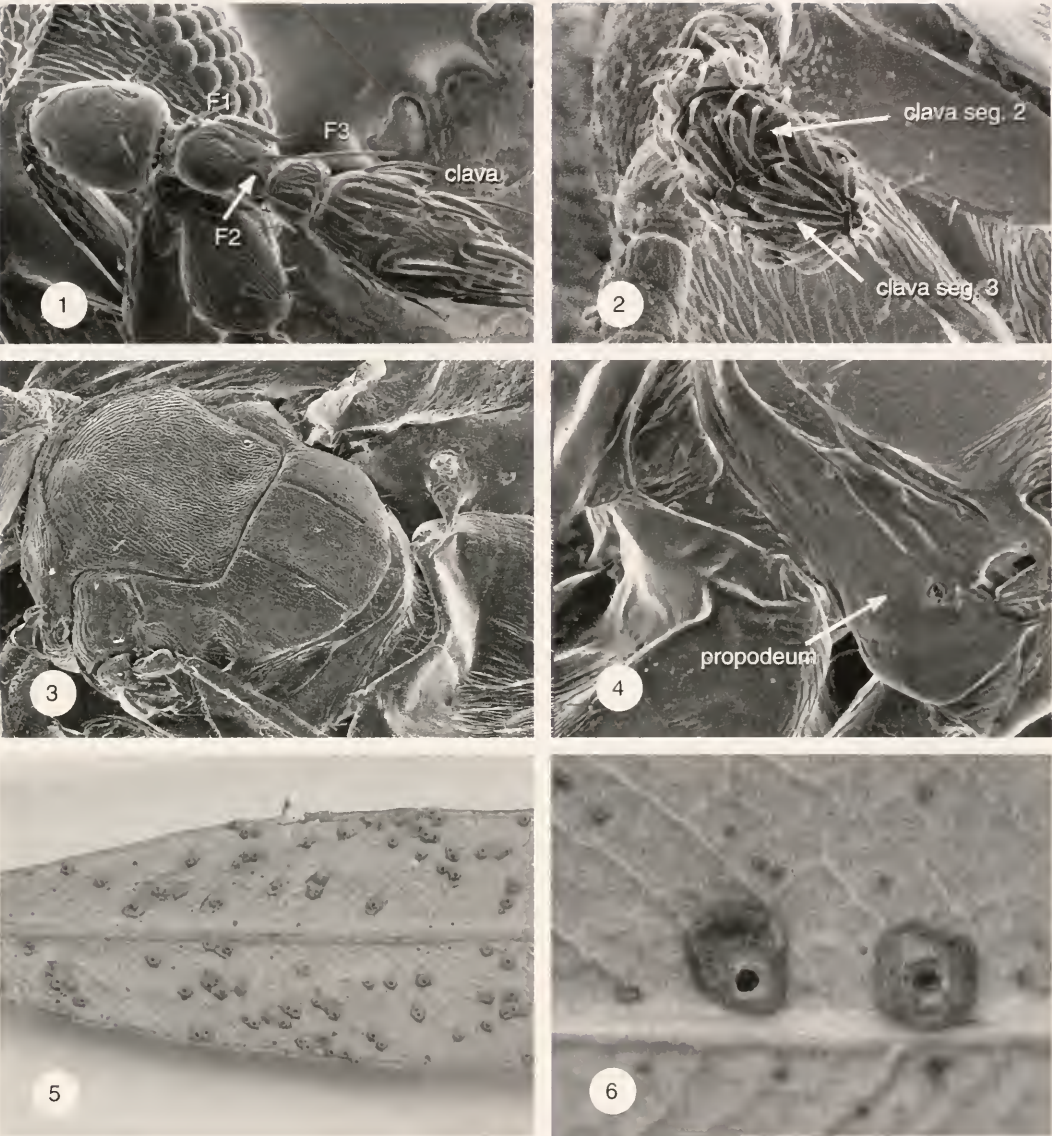
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Abstract.—*Epichrysocharis burwelli* Schauff, new species (Hymenoptera: Eulophidae) is described from specimens collected in southern California. *Epichrysocharis burwelli* forms small blister-like galls on the leaves of *Eucalyptus citriodora*. The previously described species of *Epichrysocharis* are reviewed and separated from *E. burwelli*. Evidence suggests that this species was accidentally introduced into the United States from Australia.

In early 1999, specimens of a small chalcidoid wasp were submitted to the Systematic Entomology Laboratory, USDA, by the California Department of Food and Agriculture (CDFA) for identification. These tiny wasps were found emerging from galls on the leaves of *Eucalyptus citriodora* in the Los Angeles area. Recently, their occurrence has been noted in several nurseries, and they are becoming widespread in the Los Angeles area. Study of these specimens and subsequent rearings revealed them to belong to the genus *Epichrysocharis* (Hymenoptera: Eulophidae). This genus was only known to occur in Australia and includes 3 species (Bouček 1988). After study of the types of those species it was determined that the specimens reared in California represented a species unknown to science. We take this opportunity to describe this species and present information on the known species of the genus to facilitate their identification. Given the known distribution of this genus, it is highly likely that this species was accidentally introduced into California from Australia.

The biology of *Epichrysocharis* species

had been unknown, although it was stated that they had been “associated with small galls on Eucalypt leaves” (Bouček 1988). The specimens recorded from California were reared from small blister-like galls on the leaves of *Eucalyptus citriodora* and unemerged specimens have been dissected from inside galls on the leaves. We can find no evidence that *E. burwelli* is parasitizing some other insect in or associated with the galls. It can now be confirmed that this species is a gall former. The galls themselves appear as small reddish or brownish blisters on the surface of the leaf (Figs. 5, 6). The galls are expressed on both surfaces of the leaves (that is, a single gall produces a “blister” on both surfaces) and the wasps do not seem to have a preference for one side or the other as emergence holes can be seen on both sides of a single leaf. The emergence holes are round and tend to be in the center of the gall (Fig. 6). The galls can be quite numerous and we have counted in excess of 40 in a single square centimeter of leaf surface. Whether or not this gall formation causes significant damage to the plant has not yet been assessed. However, the appearance



Figs. 1–6. 1–4. Scanning electron micrographs: 1, Female antenna, dorsolateral view. 2, Female clava, dorsoapical view. 3, Mesosoma, dorsal view. 4, Propodeum. 5–6. *Eucalyptus citriodora* leaf: 5, Surface with galls. 6, Closeup of gall showing emergence hole.

of these galls on nursery stock would most likely reduce the attractiveness of the plant and lower its market value. The wasps appear to be spreading and are now found in seven localities within Los Angeles County.

During the editing of this paper an additional series of three specimens of another small tetrastichine was reared from

Eucalyptus leaves in Santa Barbara, California. This species is readily distinguished from *Epichrysocharis burwelli*, but because of the condition and limited number of specimens I have been unable to definitively assign this species to a genus. Along with a third species of tetrastichine described by Headrick *et al.* (1995) from California, and introduced from Australia

on *Chamelaucium unciatum* (Myrtaceae), it is apparent that phytophagous species are increasingly becoming established in the U.S.

Terminology for morphology follows Gibson (1997) and LaSalle (1994).

Acronyms for museums are: (BM) Bohart Museum, University of California, Davis, CA, USA; (CNC) Canadian National Collection, Ottawa, Ontario, Canada; (QM) Queensland Museum, Brisbane, Australia; (BMNH) The Natural History Museum, London, UK; (USNM) National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA.

Epichrysocharis Girault

Epichrysocharis Girault 1913b:36. Type species, *Epichrysocharis fusca* Girault. Original designation.

Brachychrysocharopsis Girault, 1922:103. Type species, *Brachychrysocharopsis aligherini* Girault. By monotypy. Synonymy by Bouček (1988: 690).

Diagnosis.—Length generally 0.5mm or less; antenna (Figs. 1, 2) with 2 anelli, 3 funicles, all quadrate or wider than long, F1 wider than F2 or F3, F2 smaller than F3, F1 closely appressed to F2 and partially extended over and covering F2 such that in some views F2 is hidden giving the impression that the funicle is 2-segmented, clava longer than funicle; clava 3-segmented, 3rd segment with suture obliquely angled from 2nd (Fig. 2); malar suture complete; pronotum very narrow medially, overhung by anterior margin of mesoscutum and not visible from above; mesoscutum large, convex, without median longitudinal groove, adnotaular setae restricted to area near notaulus in one or two irregular lines and often with only 2–3 setae on each side; scutellum with submedian grooves and two pair of setae; propodeum very short medially, generally equal to or shorter than metanotum, with no median or subspiracular carinae; spiracle round; metasoma sessile, broadly attached to mesosoma and with no obvious

petiole, phragma generally projecting into gaster. Submarginal vein with single dorsal seta, marginal vein subequal to submarginal, stigmal vein well developed and about 1/2 length of marginal.

Epichrysocharis closely resembles a number of small Australian tetrastichines which also have very short antennae but are currently placed in the large genus *Aprostocetus*. In addition, there are other genera generally considered closely related to *Aprostocetus*, which have shortened funicles (all 3 funiculars quadrate to slightly wider than long, about the same width, and funicle about equal in length to or slightly longer than clava [see, for example, *A. (Epomphaloides) flavus* (Bouček 1988, fig. 1191)]). While we have not studied these species closely, and many are probably undescribed, one of the defining characters of *Aprostocetus* is that the raised lobe of the callus partially overhangs the outer rim of the propodeal spiracle (Graham 1987; LaSalle 1994). We have not observed this condition in the species which we place in *Epichrysocharis*.

Bouček (1988) synonymized *Epentastichus* Girault under *Aprostocetus*. The senior author has examined the type species, *Epentastichus nugatorius* Girault (QM). Unfortunately, the body of the type has been lost and only two heads, mounted on a slide, remain. These heads are in poor condition, but the antennae of these two partial specimens are very similar to *Epichrysocharis*. However, given the fragmentary nature of the specimens, and in the absence of more detailed revisionary work, we do not feel that enough evidence exists at this time to make any further nomenclatural changes regarding the placement of *E. nugatorius*. Bouček (1988) also synonymized *Epomphaloides* with *Aprostocetus*.

Several species of other genera from the Australian fauna have also been reared from or associated with galls on *Eucalyptus*. Although they were studied at the generic level by Bouček (1988), the included species have not been critically revised.

What is apparent, is that this whole complex of generic names and species is much more diverse than indicated by the few species described at this time, and that much work on the taxonomy will need to be done to increase our understanding of the limits of this group of genera.

Species of *Epichrysocharis*

Epichrysocharis aligherini (Girault)

Brachychrysocharopsis aligherini Girault 1922: 103. Transferred to *Epichrysocharis* by Bouček 1988.

Diagnosis.—Mesosoma and metasoma black; forewing with apical fringe equal to about 1/3 wing width; ovipositor about 2/3 to 3/4 length of metasoma, slightly exerted past tip of gaster. This species is distinguished by the uniform dark coloration and the elongate ovipositor which extends for well over half the length of the metasoma.

Type.—The single type specimen of this species is slide mounted. It is badly crushed and disarticulated with the head, mesosoma, metasoma, legs, and antennae scattered over the slide. The head is fragmented and the antennae mostly disarticulated and shriveled making it nearly impossible to make out the relative sizes and numbers of segments. A single forewing remains attached to the mesosoma. The other wings cannot be found. The specimen is not cleared, but a few characters can be discerned, and based on what can be seen, it appears that this species is appropriately placed in *Epichrysocharis*. There is no register number evident on the slide. Deposited in QM.

Epichrysocharis fusca (Girault)

Quadrastichus fusca Girault 1913b: 234. Transferred to *Epichrysocharis* by Girault 1913b. Isotypic with *Q. fusca*.

Diagnosis.—Body light brown or yellow, head yellow; antenna with F1, F2, and F3 all wider than long and all subequal in length. F1 and F2 each with a single lon-

gitudinal sensillum. Ovipositor about 1/3 length of metasoma. This species is distinctive because it is the only one with a longitudinal sensillum on F2.

Type.—The type (QM register no. Hy-1847) of this species is a female, slide mounted with the body minus the head under one cover slip and the head under the second cover slip. The head is badly crushed, but one antenna is clearly visible. The body is not cleared. Deposited in QM.

Epichrysocharis nigriventris (Girault)

Epentastichus nigriventris Girault 1913a: 242. Transferred to *Epichrysocharis* by Bouček 1988.

Diagnosis.—Head yellow, mesosoma yellow orange, metasoma brown to dark brown, hind femur brown, hind tibia and tarsus yellow; mesoscutum and scutellum striate reticulate; mesocutum about 2× as long as scutellum, metasoma ovate and slightly shorter than mesosoma (30:25); antenna with F1 as long as wide, 3× as long as F2, clava about 4× as long as F2 and 2× as long as wide; only F1 and clava with multiporous plate sensillae; hypopygium reaching nearly to end of metasoma.

Types.—Two specimens (QM register no. Hy-1849) of this species are point mounted on a single pin. Girault noted that the species was described from two females, but did not designate a holotype. We hereby designate as lectotype the specimen nearest the point of the card mount and the other specimen as paralectotype. The lectotype is partially submerged in glue, but not as completely as the paralectotype. The heads of both specimens have been slide mounted, and there is no way of associating any one head with one of the point mounted bodies although it seems that both specimens do belong to the same species. Deposited in QM.

Epichrysocharis burwelli Schauff, new species (Figs. 1–4)

Diagnosis.—Body brown, with face vertex, upper margin of eyes, and scrobes yellow.

low; F1 with longitudinal sensillum (Fig. 1); ovipositor about 1/2 length of metasoma, with hypopygium reaching half the length; forewing fringe about 1/4 wing width. The distinctly brown and yellow head with a uniformly brown mesosoma and metasoma and relatively short ovipositor set this species apart from the others in the genus. In addition, *E. nigriventris* has the hypopygium reaching almost to the end of the metasoma and *E. aligherini* has a longer ovipositor which is slightly exerted past the tip of the metasoma.

Description.—Female. Length 0.5–0.6mm. Color. Brown or light brown except following yellow: a small strip below each torulus, scrobes, vertex, dorsal occiput, a small thin stripe bordering the eye from about the line of the toruli up and around the back of the eye for about half its length, antennae, and apices of tibiae and usually first three tarsomeres.

Head: Face alutaceous to strigose, scobal basin nearly smooth, vertex and occiput rugose to finely alutaceous. Posterior ocelli widely separated, anterior ocellus only about 1 diameter in front of posterior ocelli and with POL about $5 \times$ OOL. Mandible with 3 distinct teeth. Toruli inserted even with bottom of eye. Antenna (Figs. 1, 2) with scape $3 \times$ as long as wide, second anellus with 2 dorsal setae, F1 slightly longer than wide (10:12) on ventral surface, as long as wide on dorsal surface, with single longitudinal sensillum, F2 $2 \times$ as wide as long, loosely appressed to F1 and partially covered dorsally by F1, F3 $1.5 \times$ as wide as long, clava $2 \times$ as long as wide with several longitudinal sensillae some of which extend past tip of clava.

Mesosoma: Pronotum reduced, not visible medially from above. Mesoscutum, scutellum, dorsellum, and lateral propodeum finely alutaceous or coriaceous (Fig. 3). Mesoscutal midlobe with 2 or 3 minute, inconspicuous setae at notaular margin. Dorsellum lightly alutaceous. Propodeum smooth to very lightly alutaceous laterally (Fig. 4), with two minute setae laterad of

spiracle. Forewing $2 \times$ as long as wide, with longest marginal fringe seta 1/4 width of wing. Ratio of costal cell : parastigma : submarginal vein : marginal vein : stigmal vein 20:15:25:28:15.

Metasoma: Slightly shorter than mesosoma, ovate and slightly longer than wide, rounded posteriorly. First tergum nearly smooth medially, rest of mesosoma uniformly, densely rugose reticulate. Ovipositor about 1/2 length of metasoma. Hypopygium reaching about 1/2 length of metasoma.

Male.—Similar to female.

Types.—Holotype female on slide with data: California, Los Angeles Co., Monterey Park, Wilcox & 60 Fwy (s. side), 11 May, 1999. Reared *Eucalyptus citriodora*. Coll. D. Humphreys and M. Suim. Deposited in USNM. 52 female and 1 male paratypes with same data. Paratypes deposited in BMNH, BM, CNC, QM.

Etymology.—The species epithet honors Dr. C. Burwell, Queensland Museum without whose help this study could not have been completed.

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A Revision of the Panurgine Bee Genus *Arhysosage* (Hymenoptera: Andrenidae)

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Abstract.—The South American bee genus *Arhysosage* Brèthes (Panurginae: Calliopsini) is revised. In addition to the previously recognized *Arhysosage flava* Moure, *A. cactorum* Moure, *A. ochracea* (Friese), and *A. bifasciata* (Friese) (**new combination**), two new species are described: *A. atrolunata* Engel and *A. zamicra* Engel. *Arhysosage germana* Moure is newly synonymized with *A. ochracea* and *A. melanothricha* Moure is synonymized with *A. cactorum*, while *A. bifasciata* is resurrected from synonymy under *A. ochracea* with *Camptopoeum opuntiarum* Jörgensen as a junior subjective synonym (**new synonymies**). The genus is newly diagnosed and a key to the currently recognized species is presented. The name appearing in the literature as *A. xanthina* is a *nomen nudum*. The phylogenetic position of the genus among other calliopsine bees is briefly summarized as are relationships among the species. A cladistic analysis of *Arhysosage* produces a single tree with the following hierarchy: *A. cactorum* (*A. flava*, *A. zamicra* (*A. ochracea* (*A. atrolunata*, *A. bifasciata*))). Biological information on *Arhysosage* is summarized. The genus is presently known from Argentina, southern Brazil, Bolivia, and Paraguay and is apparently a specialist on Cactaceae (presently recorded from *Echinocactus*, *Echinopsis*, *Gymnocalycium*, *Notocactus*, *Opuntia*, and *Trichocereus*).

Bees of the genus *Arhysosage* Brèthes (1922) are among the most distinctive of the South American panurgines, being characterized by the fairly robust size of most individuals, large heads of males, and mostly yellow body coloration (Fig. 1). Individuals can be readily captured at flowers of various cactus genera (e.g., *Gymnocalycium*, *Notocactus*, *Opuntia*, &c.) upon which they are presumably oligolectic (Schlindwein 1992, Schlindwein and Wittmann 1995). Outside of their affinity for cactus flowers, however, the biology of *Arhysosage* species has not been the focus of any published study, although Schlindwein and Wittmann (1995) give a few details of mating behavior in *Arhysosage*. Their observations indicate that mating is initiated at cactus flowers. Males search flowers for females, sometimes staying motionless in inflorescences for up to seven minutes. Once a female appears, the

male grabs her waist with his long mandibles and initiates copulation. The couple frequently continues mating during flight and may visit several flowers throughout the encounter, with the female continuing to forage the whole time. Such mating behavior is reminiscent in some respects to that described for *Perdita* (*Macrotera*) *texana* (Cresson 1878). Like *Arhysosage*, this group is oligolectic on Cactaceae (Snelling and Danforth 1992, Neff and Danforth 1992) and also demonstrates a dramatic head-size polymorphism in males that, among other uses, allows males to grasp females during copulation (Danforth and Neff 1992). Future field work on *Arhysosage* species should explore possible ethological-morphological associations in males as has been done for *Perdita*.

The genus was established by Brèthes (1922) for an enigmatic bee species in northern Argentina, but its systematic po-



Fig. 1. Dorsal habitus of male *Arhysosage ochracea* (Frieze).

sition in the Panurginae remained unrecognized until the late 1950s when Moure and Michener were able to examine the type series (Moure 1958). Brèthes was unaware that Frieze (1908) had already described the species in *Camptopoeum* Spinola (1843). Cockerell in 1940 described the species for a third time. Timberlake (1952a) was the first to place the genus in the Calliopsini but under the name *Rui-ziella* as he was unaware of, or not able to interpret, Brèthes' work. Moure (1958) correctly established the name of the genus, described two new species, and briefly discussed its placement in the Panurginae, although he disagreed with Timberlake's assignment of the genus to Calliopsini. Following a phylogenetic study of the

Panurginae based on the external morphology of adults, Ruz (1986, 1991) placed *Arhysosage* in the tribe Calliopsini together with four other genera. *Arhysosage* was placed as the sister to a clade consisting of *Callonychium* Brèthes (1922) and *Spinoliella* Ashmead (1899) (Fig. 2). The three genera were grouped on the shared presence of yellow metasomal markings, the weak or absent transverse ridge on the male labrum, absence of an inflection at the female labral apex, position of the male antennal sockets on the lower third or fourth of the face, broken pattern of keirotichia on the inner surface of the female metatibia, and absence of a volsella. *Arhysosage* was excluded from the *Callonychium* + *Spinoliella* clade by the primitive presence

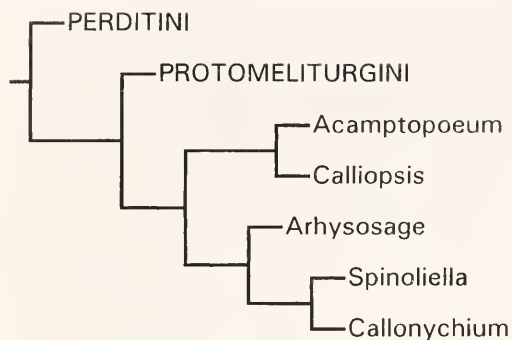


Fig. 2. Phylogeny of tribe Calliopsini (after Ruz 1991) indicating the position of *Arhysosage* and related genera. Perditini and Protomeliturgini are out-group tribes.

of a slightly convex lower paraocular area, presence of keirotichia on most of the inner surface of the male metatibia, patterning of the keirotichia on the inner surface of the female metatibia, composition of the metatibial scopa of only moderately abundant hairs, absence of a lateral ridge on the female S6, gonostylus being one-half to one-third the length of the gonocoxa, and absence of internal sclerotization in the aedeagus. While *Arhysosage* is known only in Argentina, southern-most Brazil, Paraguay, and southeastern Bolivia, both *Callonychium* and *Spinoliella* are somewhat more widely distributed. *Callonychium* occurs in Argentina, Brazil, Chile, Paraguay, and Peru (Ruz 1991, Toro and Herrera 1980) while *Spinoliella* is distributed in Chile (Ruz 1991, Toro 1995, Toro and Ruz 1972), Argentina, and Peru (Engel unpubl. data). Given the present collection localities for *Arhysosage* it seems likely that the genus will someday be discovered in Uruguay.

Herein I present a revision of *Arhysosage* including a generic description modified from that provided by Ruz (1991), incorporating the changes that result from addition of new species to the genus. A key to calliopsine genera distinguishing *Arhysosage* has been presented by Ruz (1991) and Michener (in press).

MATERIALS AND METHODS

Morphological terminology generally follows Michener (1944) with additions for mandibular structure provided by Michener and Fraser (1978); also, I use anal vein in place of vannal. The abbreviations F, S, and T are employed for flagellomere, metasomal sternum, and metasomal tergum, respectively. The most common species, *A. ochracea*, is described in detail and all other descriptions are referenced to this one so as to avoid repetition.

A total of 479 specimens (215 ♀♀, 264 ♂♂) were examined during the course of this study. Specimens were provided by the following institutions: AMNH, American Museum of Natural History, New York, New York, J. G. Rozen, Jr., and M. G. Rightmyer; BMNH, The Natural History Museum (British Museum), London, United Kingdom, G. Else and C. Taylor; CAS, California Academy of Sciences, San Francisco, California, W. J. Pulawski and R. L. Zuparko; CTMI, Central Texas Melittological Institute, Austin, Texas, J. L. Neff; CUIIC, Cornell University Insect Collection, Ithaca, New York, J. K. Liebherr and E. R. Hoebeke; LACM, Natural History Museum of Los Angeles County, Los Angeles, California, R. R. Snelling; MACN, Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina, A. Roig-Alsina; MLPA, Museo de La Plata, Universidad Nacional de La Plata, La Plata, Argentina, J. A. Schnack; NHRS, Naturhistoriska Riksmuseet, Stockholm, Sweden, T. Pape; PCIA, Personal Collection of Isabel Alves dos Santos, São Paulo, Brazil; SEMC, Snow Entomological Collection, Natural History Museum, University of Kansas, Lawrence, Kansas, R. W. Brooks and C. D. Michener; USNM, United States National Museum of Natural History, Smithsonian Institution, Washington, D.C., R. J. McGinley, M. Mello, and D. G. Furth; ZMHB, Zoologisches Museum an der Humboldt-Universität, Berlin, Germany, F. Koch.

Table 1. Character matrix and character descriptions used in cladistic analysis of the internal phylogeny of *Arhysosage*. *Callonychium* and *Spinoliella* are used as outgroups. Refer to Material and Methods for details of analysis. 1. Inner hind tibial spur: (0) straight, (1) curved. 2. Compound eyes below: (0) parallel, (1) diverging. 3. Metasoma: (0) much broader than head, (1) as broad as head. 4. Male clypeal apex: (0) straight between lateral corners, (1) gently convex between lateral corners. 5. Male pygidial plate emargination: (0) absent, (1) present. 6. Male S7 lateral processes: (0) broad, expanded towards base, (1) narrow, not expanding towards base. 7. Aedeagus: (0) shorter than penis valves, (1) as long as or longer than penis valves.

Taxa	Characters
	1234567
<i>A. atrolunata</i>	1111111
<i>A. bifasciata</i>	1111111
<i>A. flava</i>	1110101
<i>A. ochracea</i>	1111101
<i>A. cactorum</i>	1110000
<i>A. zamicra</i>	1110101
<i>Spinoliella</i>	0000000
<i>Callonychium</i>	0000?10

A cladistic analysis of *Arhysosage* species was undertaken. Species of *Callonychium* and *Spinoliella* were used as outgroups. Seven characters were identified and coded for the taxa employed. The single interrogative mark presented in the data matrix (Table 1) is a polymorphism for this character in *Callonychium* and not missing information. Character descriptions are given with the data matrix (Table 1). The data matrix was constructed in DADA (Nixon 1995) and analyzed using the *ic** command in HENNIG86 (Farris 1988). Trees were visualized and printed using CLADOS (Nixon 1993).

SYSTEMATICS

Genus *Arhysosage* Brèthes

Arhysosage Brèthes 1922: 121. Type species: *Arhysosage johnsoni* Brèthes 1922 (= *Camptopoeum ochraceum* Friese 1908), monobasic. Ruz 1991: 238.

Ruiziella Timberlake 1952a: 105. Type species: *Camptopoeum ochraceum* Friese 1908, original designation. Preoccupied (*nec* Cortés 1951).

Ruziapis Timberlake 1952b: 528. Type species: *Camptopoeum ochraceum* Friese 1908, autobasic. Replacement name for *Ruiziella* Timberlake 1952a (*nec* Cortés 1951) and *lapsus calami* for *Ruizapis* Timberlake 1953 (justified emendation).

Ruizapis Timberlake 1953: 598. Type species: *Camptopoeum ochraceum* Friese 1908, autobasic. Justified emendation of *Ruziapis* Timberlake 1952b (*lapsus calami*).

Diagnosis.—*Arhysosage* differs from other South American panurgines by the ventral divergence of the compound eyes (Figs. 10, 12, 14–15, 18, 20, 22, 24), the broad heads (same figures as just mentioned), the curved inner metatibial spur (Fig. 6), and the mostly yellow body coloration (e.g., Fig. 1).

Description.—Head broader than long in frontal view, broader than thorax (Fig. 1). Glossa longer than prementum, slender; paraglossa shorter than suspensorium; first segment of labial palp less than twice as long as combined lengths of segments 2–4. Maxillary blade longer than prepalpal part of galea; galeal comb absent. Labrum less than twice as broad as long, partially or entirely setose. Apical margin of clypeus with variably developed projection just outside lateral labral margin. Epistomal sulcus forming an obtuse angle (Figs. 9–10). Inner subantennal suture angulate (Figs. 9–10); subantennal area wider than length of inner suture and than antennal socket; anterior tentorial pit near middle of outer subantennal suture (Fig. 16). Antennal socket far below middle of face (Fig. 15). Lower median paraocular area slightly convex. Facial fovea strongly impressed, narrow (Fig. 10). Median ocellus set below upper tangent of compound eyes. Vertex convex. Mesepisternum with flattened anterior-facing surface reduced; preëpisternal groove distinguishable only above scrobal level, continued downward as black line (difficult to see on dark integument). Forewing with cu-a as long as or longer than second abscissa of M + Cu; 1m-cu well distad 1r-m; 2m-cu basad 2r-

m; pterostigma longer than and slightly wider than prestigma, border within marginal cell straight; apex of marginal cell obliquely and broadly truncate, longer than distance from apex to wing tip; first submarginal cell as long as or longer than second submarginal cell (Fig. 1). Hind wing with cu-a slightly less than one-half to one-third as long as second abscissa $M + Cu$; 10 distal hamuli arranged in a single series. Protarsomeres 2–4 unmodified; malus of antenna cleaner pectinate. Mesotibial spur half as long as or longer than mesobasitarsus, apex distinctly curved, finely serrate. Mesobasitarsus about as long as probasitarsus and shorter than metabasitarsus, tarsomeres 2–4 unmodified. Metatibial spurs curved at apices, outer spur as long as or longer than inner spur; teeth small. Metatarsus unmodified. Claws deeply cleft. Basal area of propodeum slightly longer than metanotum, with exceedingly fine striae along apical margin, depressed medially. Metasoma with yellow bands very extensive to incomplete or absent; terga without setal bands; lateral fovea of T2 slightly depressed. Pubescence generally short and sparse; appressed hairs on most of dorsum of mesosoma and metasoma. Punctures generally very fine and dense, nearly contiguous on mesoscutum. **Male:** Most of head and thorax yellow (Figs. 1, 10, 12, 14, 18, 22, 24). Labrum flat, with slight transverse ridge. Mandible arcuate, longer than compound eye (except in *A. zanicra*), upper margin with prebasal projection (Fig. 18: arrow) and subapical tooth (Fig. 10). Length of clypeus more than four times width, gently protuberant. Flagellum unmodified, much shorter than head; F1 as long as or slightly longer than F2, about as long as broad. Inner orbits of compound eyes markedly divergent below. Pronotum with dorsal preapical ridge rounded, strong. Length of probasitarsus five times width. Metatibia with keirotichia on most of inner surface but sparser ventrally. Basitibial plate with borders

well-defined. Rami of claws subequal in length. Metasoma wider than thorax (Fig. 1); T2–5 with gradulus posterolaterally long (surpassing middle of each tergum), carinate, and with postgradular depression narrow, shallow; posterior marginal areas of T1–5 minutely setose; pygidial plate well developed, abruptly elevated and carinate laterally towards apex; hemitergum hexagonal; S4–5 with apical margins slightly and broadly concave medially; S6 distally bilobed, with small median V-shaped emargination; S7 with two short, finger-like apicolateral projections, proximal arms long and forming a U (Figs. 26–31); S8 with long, clavate apico-median projection, abruptly separated from basal part which has weak median ridge dorsally (Figs. 32–37). Gonocoxal apodeme not inflexed; gonocoxa short, squared, completely fused both dorsally and ventrally; gonostylus short, finger-like, fused to gonocoxa; volsella apparently absent or indistinguishably fused to gonocoxa; penis valve long, tapered toward apex, dorsally fused together by small, narrow bridge; aedeagus proximally wider and fused to valve, distal half well sclerotized ventrally (Figs. 38–45). **Female:** Yellow areas of head variable in size. Labrum nearly flat. Length of clypeus three times width, distinctly protuberant. Inner orbits of compound eyes only slightly divergent below. Pronotum with dorsal preapical ridge rounded, weak. Length of probasitarsus four times width. Metatibia longer than metabasitarsus; inner surface with keirotichia in patch at base and apex, sparse or absent toward dorsal margin, absent ventrally. Metatibial scopa of moderately dense and apparently simple, but minutely branched setae. Inner ramus of claws shorter than outer. Posterior marginal areas of T1–4 minutely setose; T7 not expanded dorsally but with conspicuous ventral proximal projection; S1–5 minutely setose, as in male, but setae somewhat longer and denser; S6 with basal spine-like sclerotization, lateral margin with

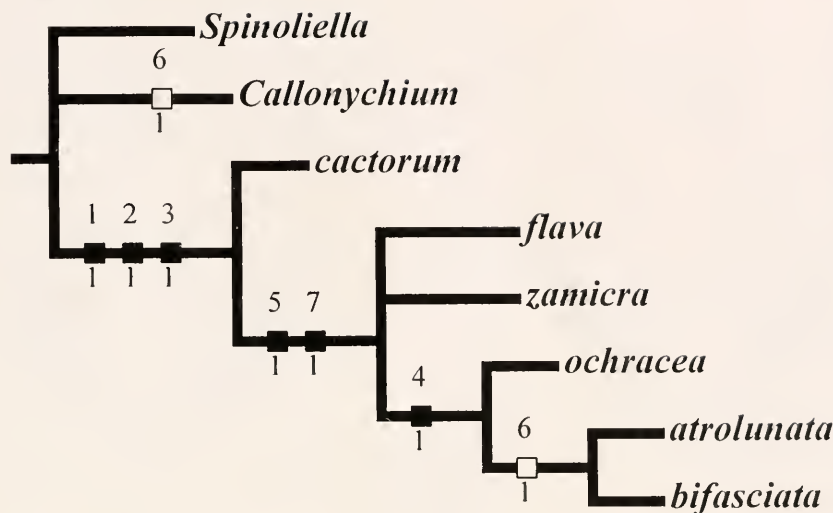


Fig. 3. Phylogeny of *Arhysosage* species (Length 8, C.I. 87, R.I. 90). *Callonychium* and *Spinoliella* are outgroup genera. Black bars indicate unreversed forward transitions while white bars indicate homoplastic characters.

strong curved ridge, apical margin concave medially, apically with a well-defined, curved and dense band of curved setae. Sting short, not reaching stylus apex.

Biological notes.—Species of *Arhysosage* are oligolectic on Cactaceae. The long, curved mandibles of males seem to be a modification for grasping the female during mating, while the mostly yellow body coloration appears to be an adaptation for minimizing visibility in flowers, which are generally yellow or off-white. Immature stages of *A. flava* have been discovered by Jerome G. Rozen, Jr. (AMNH) and will be treated in a forthcoming paper concerning the immature stages of Calliopsini (Rozen and Engel in prep.).

Phylogeny.—The result of a cladistic analysis for *Arhysosage* (see Material and Methods) is presented in figure 3. A single tree resulted from analysis of the data matrix (Table 1); the topology had a length of 8, a C.I. of 87, and an R.I. of 90. This analysis places *A. cactorum* as the sister to the remainder of *Arhysosage*. Two species, *A. flava* and *A. zamicra*, were unresolved in a polytomy (Fig. 3). These species are exceedingly similar with *A. zamicra* possess-

ing a number of autapomorphic features which allow for its recognition but fail to confidently group it with any other species of *Arhysosage* [i.e., whether sister to the remainder of *Arhysosage* (exclusive of *A. cactorum*), to *A. flava*, or to *Arhysosage* exclusive of *A. flava* and *A. cactorum*].

***Arhysosage ochracea* (Fries)**
(Figs. 1, 5, 8, 17–21, 26, 32, 38, 49)

Camptopoeum ochraceum Fries 1908: 29. Examined (ZMHB).

Arhysosage johnsoni Brèthes 1922: 122.

Camptopoeum castellani Cockerell 1940: 1. Examined (AMNH).

Ruiziella ochracea (Fries); Timberlake 1952a: 105.

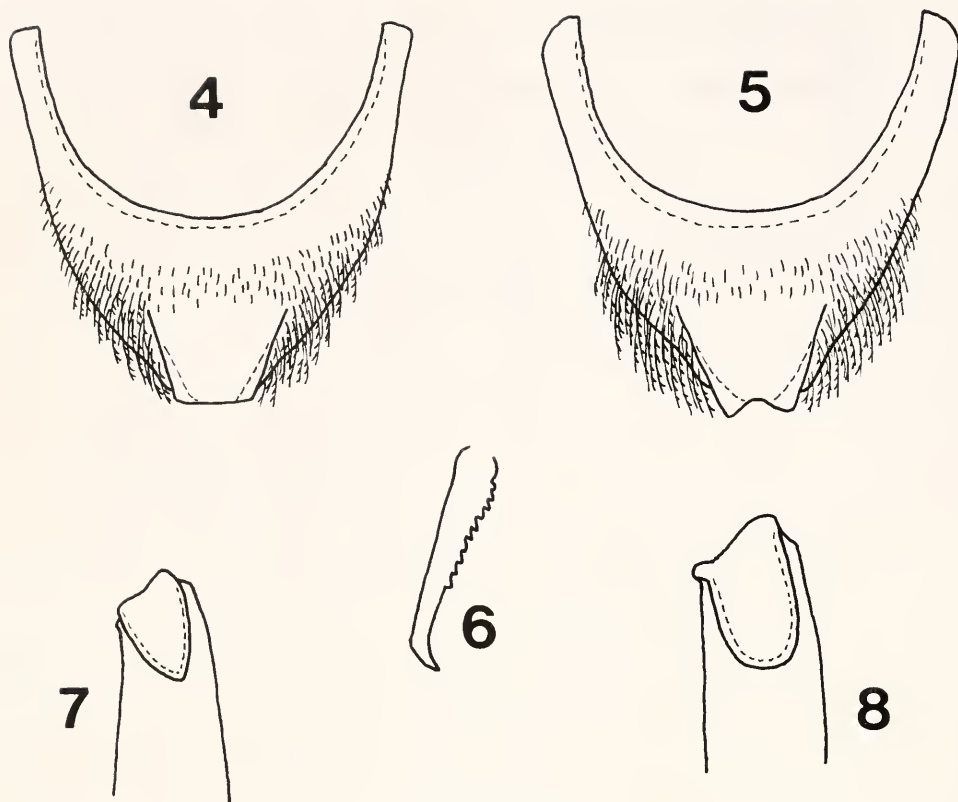
Ruiziella castellani (Cockerell); Timberlake 1952a: 105.

Arhysosage ochracea (Fries); Moure 1958: 44.

Arhysosage germana Moure 1958: 47. **New synonymy.** Examined (SEMC).

Diagnosis.—The species can be most readily separated from other *Arhysosage* species by the strong banding of the metasoma (Fig. 1).

Description.—**Male:** Total body length 8.0–12.6 mm; forewing length 5.8–7.2 mm. Head width 2.3–4.0 mm, length 1.6–3.0



Figs. 4-8. Characteristics of *Arhysosage*. 4, Pygidial plate of male T7 of *Arhysosage cactorum* Moure. 5, Pygidial plate of male T7 of *A. ochracea* (Friese). 6, Inner hind tibial spur of *A. cactorum*. 7, Basitibial plate of *A. cactorum*. 8, Basitibial plate of *A. ochracea*.

mm. Mandible longer than compound eye; inner tooth well-defined, not particularly strong, somewhat rounded (Figs. 18, 20). Upper interorbital distance 1.3-2.3 mm, lower interorbital distance 1.5-3.1 mm. Intertegular distance 1.4-2.5 mm. Basitibial plate apex broadly rounded (Fig. 8). Apex of pygidial plate slightly emarginate (Fig. 5). Apex of penis valve bending ventrally (Figs. 45-49); aedeagus reaching, or very near to, apex of penis valve (Figs. 38-42, 45-49); terminalia otherwise as depicted in figures 26, 32, 38, and 49.

Mandible mostly smooth with a few faint punctures on dorsal surface running from base in a narrow band to point of inner tooth; a few faint punctures in outer interspace, disappearing by point where

outer ridge and condylar ridge meet; ventral surface with similar punctures as those of dorsal surface and disappearing by about the same point. Clypeus with faint, coarse punctures scattered over surface, integument otherwise smooth. Subantennal areas smooth and impunctate. Supraclypeal area below antennal sockets and between inner subantennal sutures as on clypeus; between antennal sockets punctures well-defined, smaller, and nearly contiguous. Scape punctured as on supraclypeal area between antennal sockets. Face lateral to outer subantennal sutures and below level of antennal sockets as on clypeus; at level of antennal sockets punctures become smaller, well-defined, and gradually more closely spaced until nearly contiguous by level just above antennal

sockets; remainder of face and vertex with such fine, well-defined punctures, nearly contiguous. Gena as on vertex except punctures becoming faint on lower half and separated by 1–2 times puncture width, integument otherwise smooth, punctures also become fainter posteriorly near preoccipital area. Postgena impunctate and smooth. Pronotum with minute, well-defined punctures on dorsal surface along border with mesoscutum, medially and anteriorly on collar integument impunctate and imbricate; lateral surfaces smooth and impunctate except on pronotal lobe which has a few minute punctures. Mesoscutum and scutellum with small, well-defined, nearly contiguous punctures. Tegula similar to mesoscutum except punctures quite faint. Metanotum with scattered faint, coarse, punctures, integument between faintly imbricate. Preëpisternal area as on mesoscutum except punctures becoming exceedingly faint and more widely spaced ventrally; mesepisternum with faint, coarse punctures separated by less than puncture width, integument between smooth, punctures becoming more widely spaced along posterior border and fainter ventrally; metepisternum with faint, minute punctures separated by width or less, integument between smooth. Basitibial plate with minute punctures separated by less than a puncture width. Propodeal lateral surface with minute, well-defined punctures separated by 1–3 times puncture width, integument between smooth; posterior surface with minute punctures separated by width or less, integument imbricate. Anterior surface of T1 faintly imbricate, remainder of surface minutely punctured, punctures nearly contiguous except apical margin imbricate and impunctate; T2–6 minutely punctured, punctures nearly contiguous except apical margins imbricate and impunctate; T7 imbricate; sterna imbricate with scattered, faint punctures.

Head mostly yellow except facial fo-
veae black and two spots on clypeus dark

brown to black. Inner tooth, subapical tooth, and mandibular apex reddish brown to black. Proboscis light brown; hypostomal fossa as well as bordering areas of postgena and preoccipital area dark brown to black. Labrum yellow. Flagellum light brown. Pronotum yellow. Mesoscutum, tegula, scutellum, and metanotum yellow. Preëpisternum, mesepisternum, and metepisternum yellow except on ventral-facing surface dark brown to black; propleuron dark brown to black except posterolateral corner yellow. Inner halves of procoxa dark brown to black, remainder yellow; protrochanter yellow except ventral border brown; profemur yellow with brown spot on inner and ventral surface at base; remainder of foreleg yellow; inner halves of mesocoxa dark brown to black; ventral and inner borders of mesotrochanter and mesofemur brown; ventral border of mesotibia light brown; remainder of midleg yellow; metacoxa and metatrochanter mostly dark brown or black except yellow on dorsal borders; metafemur with inner and outer borders brown, remainder yellow; inner border of metatibia and metabasitarsus light brown, remainder yellow; claws reddish brown at apices; mesotibial spine and metatibial spurs amber. Wing membrane hyaline; veins amber to dark brown. Propodeum yellow except basally bordering metanotum dark brown to black with mediolongitudinal, narrow line of black running from the basal area onto the posterior surface and ending medially at marginal area of propodeum. Mediolongitudinal line of T1 anterior surface amber, remainder yellow except apical margin amber; T2–6 yellow except graduli, areas lateral to graduli, and apical margins amber, although yellow areas on central disc become gradually and progressively narrower on T3–6 until mostly obscured on T6 by overhang of preceding tergum; T7 amber; sterna amber with dark brown on central discs except medial amber interruptions on S3–5.

Pubescence generally sparse, golden, moderately long, and simple. Particularly dense areas of long setae along apicolateral margins of clypeus, just above and lateral to antennal sockets, on postgena, and on ventral borders of preoccipital area. Pronotum generally without hairs except at pronotal lobe; metanotum with mat of shorter, more dense hairs intermixed with moderately long, sparse hairs. Mesotibia and tarsus with short, stiff, amber setae along outer borders; metafemur with similar setae on outer apex; metatibia and tarsus with longer, stiff, amber setae on outer surfaces. Terga with sparse hairs except lateral to pygidial plate where they are long, dense, frequently branched, and amber to fuscous; sterna similar except patches of long, amber to fuscous hairs on either side of apical cleft of S6.

Female: As described for the male except as follows: Total body length 7.0–10.9 mm; forewing length 3.9–6.3 mm. Head width 1.9–2.9 mm, length 1.5–2.5 mm. Upper interorbital distance 1.2–1.9 mm, lower interorbital distance 1.3–2.2 mm. Intertergular distance 1.3–2.0 mm. Pygidial plate in profile straight or gently curved ventrally towards apex; dorsally gently tapering to narrowly rounded apex.

Clypeus with faint, coarse punctures scattered over surface, most faint centrally, integument otherwise smooth. Supraclypeal area as on clypeus. Scape punctured as on upper half of face. Face outside of outer subantennal sutures and below level of antennal sockets as on clypeus although punctures slightly smaller and more faint; at level of antennal sockets punctures becoming smaller, well-defined, and gradually more closely spaced until separated by puncture width or less by level just above antennal sockets; remainder of face and vertex with such fine, well-defined punctures. Gena with scattered faint punctures, integument otherwise smooth, punctures become exceedingly faint near preoccipital area and postgena. Tegula imbricate.

Face colored as in figures 17 and 19. Gena yellow. Proboscis light brown; hypostomal fossa, postgena, and preoccipital area dark brown to black. Labrum brown. Antenna light brown. Pronotum black except pronotal lobe and posterior median border yellow. Mesoscutum black except two longitudinal stripes and border with tegula yellow. Scutellum yellow except anterior border and median transverse band black, small longitudinal median black band connecting these two black areas; axilla black. Tegula and metanotum yellow. Pleura black except metepisternum yellow. Propodeum as in male except lateral surface bordering metepisternum dark brown to black.

Pubescence generally sparse, golden, moderately long, and simple. Particularly dense areas of long setae along apicolateral margins of clypeus, just above and lateral to antennal sockets, on postgena, and at base of stipes. Terga with sparse hairs except apex of T5 and lateral to pygidial plate with long, dense, frequently branched, amber hairs; sterna similar except borders of long, amber hairs on apical sterna.

Variation.—Areas described in the male as dark brown to black can vary to light brown or even yellow (except facial foveae and clypeal spots). Similarly the areas described as black in the female can sometimes be lighter and appear as dark brown. The relative widths of the yellow areas on the terga can vary dramatically as well. There is, however, always some yellow banding present on T1–3. In females, color variation is more dramatic as is demonstrated by the facial patterns depicted in figures 17 and 19 and by the fact that the amber bands of the metasoma can be quite broad and variable from light reddish brown to nearly black.

Holotype.—ARGENTINA: **Mendoza:** ♀, 24 November 1906, Jensen (ZMHB).

Additional material.—ARGENTINA: **Catamarca:** Joyango-Colpes Site, Int. Biol. Program, 24 October 1972, J. L. Neff, on *Opuntia sulphurea* (1 ♀ 1 ♂ CAS). Andalgala,

IBP Program, Desert Scrub Site, J. L. Neff, on *Opuntia sulphurea*, various dates: 20, 24, 31 October 1972, 27, 31 January 1973 (4♀ 9♂♂ CAS). Andalgala Desert Site, IBP, J. L. Neff (1♀ 3♂ CUIIC). El Pucara, IBP Program, Research Site, J. L. Neff (1♂ CUIIC). Londres, 16 November 1973, J. L. Neff (1♀ CUIIC). Santa Maria, 18 January 1973, J. L. Neff (1♂ CUIIC). Andalgala Desert site, 2 November 1973, J. L. Neff, on *Opuntia sulphurea* (1♀ 2♂♂ CTMI). Santa Maria, 11 km S. Punta [de] Balasto, 15 January 1986, J. L. Neff, on *Gymnocalycium* sp. (2♂♂ CTMI). Andalgala Desert site, 10 December 1973, J. L. Neff, on *Opuntia glomerata* (1♀ CTMI). Andalgala IBP Program, Desert scrub site, 31 January 1973, J. L. Neff, on *Trichocereus terscheckii* (1♂ CTMI). Andalgala IBP Program, Desert scrub site, 31 January 1973, J. L. Neff, on *Echinopsis leucantha* (1♀ CTMI). Cuesta Minos Copillita, 21 December 1973, J. L. Neff, on *Opuntia sulphurea* (1♂ CTMI). Andalgala Desert site, IBP, J. L. Neff, on *Opuntia sulphurea*, various dates: 20, 28, 31 October, 1, 6–7, 10, 12, 21, 24 November 1972 (10♀ 9♂♂ LACM). Andalgala Int. Biol. Prog., 4 November 1972, J. L. Neff, on *Senecio flagellisetis* (2♂♂ AMNH). El Desmonte, 25 November 1993, J. G. Rozen (1♂ AMNH). Joyango-Colpes site, IBP, 2 December 1972, J. L. Neff, on *Opuntia sulphurea* (1♂ AMNH). Andalgala, IBP, 11 December 1972, J. L. Neff, on *Trichocereus terscheckii* (1♂ AMNH). El Desmonte, 23–24 November 1989, J. G. Rozen and A. Roig-Alsina (4♂♂ AMNH). San Fernando, 3–6 November 1989, J. G. Rozen and A. Roig-Alsina (1♂ AMNH). El Desmonte, 1 December 1989, J. G. Rozen and A. Roig-Alsina, on *Opuntia* sp. (1♂ AMNH). Rio del Valle, 580 m, 5 November 1951, F. Plaumann (1♀ 1♂ AMNH). Andalgala, IBP, Desert scrub site, J. L. Neff (2♀ 2♂ AMNH). Andalgala Desert site, 24 November 1972, J. L. Neff, on *Opuntia sulphurea* (1♀ AMNH). Andalgala Desert site, 20 December 1972, J. L. Neff, on *Opuntia quimilo* (1♀ AMNH). Andalgala, 28 November 1971, D. J. Brothers (13♀ 8♂♂ SEMC). Andalgala, IBP Program, Desert scrub site, 31 January 1973, J. L. Neff, on *Opuntia sulphurea* (2♂♂ SEMC). Rio del Valle, 580 m, 3 November 1951, F. Plaumann (14♀ 9♂♂ SEMC). November 1951, Foester [sic?], J. Foerster? (3♀ 2♂♂ SEMC). Recreo, December 1951, F. H. Walz (20♀ 1♂ SEMC, 3♂♂ USNM, 2♀ 2♂ BMNH, 2♀ 1♂ AMNH). El Pucara, IBP Program research site, 1 January 1974, J. L. Neff, on *Opuntia sulphurea* (2♀ 1♂ SEMC). Londres, 10 November 1973, J. L. Neff (1♀ SEMC). Londres, 15 November 1998, Rozen, Ugarte, Navarrete (4♀ 8♂♂ AMNH). **Cordoba:** Jesus Maria, 3 December 1973, J. L. Neff, on *Opuntia sulphurea* (1♂ CTMI). **Cordoba-San Luis border:** January 1939, A. Castellanos (1♂ AMNH: holotype of *C. castellani*; 1♀ USNM: paratype of *C. castellani*). **La Rioja:** Iliar., February 1934, M. Gomez (2♀ 2♂ SEMC, 1♀ CUIIC). San Blas to Chilceto, 30 November 1983, L. E. Peña (1♂ AMNH). 14 km W Schaqui, 26 November 1989, J. G. Rozen and A. Roig-Alsina, on *Opuntia* sp. (2♀ 6♂♂ AMNH). 14 km W Schaqui, 29 November 1989, J. G. Rozen and A. Roig-Alsina, on white *Opuntia* sp. (3♀ 1♂ AMNH).

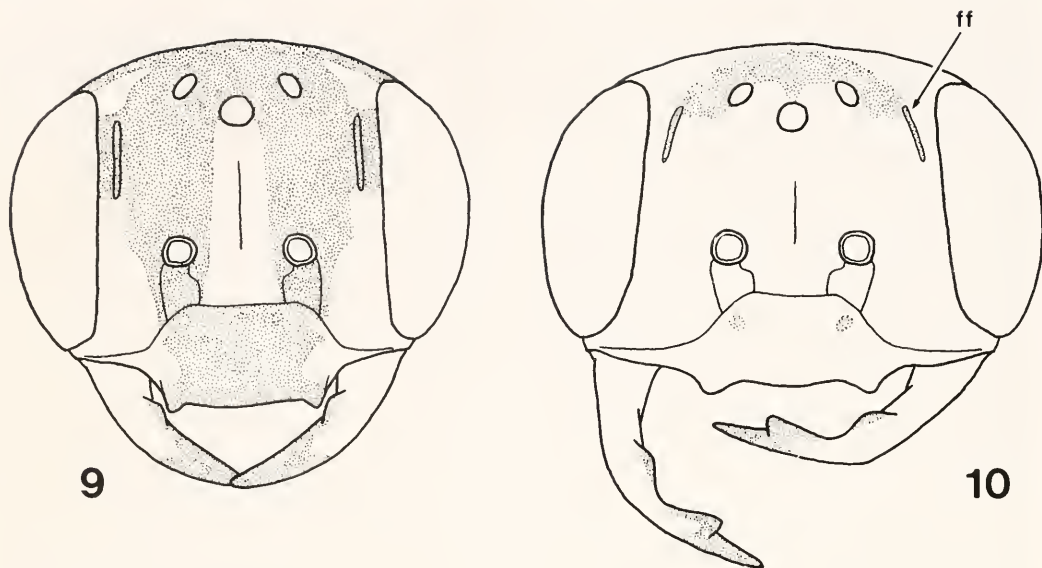
Same data as previous except on yellow *Opuntia* sp. (3♀ 9♂ AMNH). Dique, Los Sauces, December 1951, F. H. Walz (1♂ SEMC). **Mendoza:** 28 November 1906 (1♀ USNM, 1♀ NHRS). 15 November 1906 (1♂ NHRS). 10 November 1906, H. V. Jensen (1♂ ZMHB). 24 November 1906 (1♂ ZMHB). Dto. Lujan, Cerro Cacheuta, December 1972, A. Roig-Alsina (1♂ MACN). 21 November 1906, Jensen (1♀ CAS). P. Herbst collection, ex. Reed (1♂ CAS). 15 km W. Mendoza, 1000 m, 7–8 December 1979, C. and M. Vardy, B.M. 1980–67 on *Trichocereus candicans* or *Opuntia sulphurea* (5♀ 9♂♂ BMNH). 21 November 1906 (1♀ AMNH). Tucumán, 2000 m (1♂ AMNH). **Salta:** 4 km NE Alemania, 13 November 1993, J. G. and B. L. Rozen, on *Opuntia* sp. (2♂♂ AMNH). Cruz Quemada, 31 km S General Gumes, 10 November 1989, J. G. Rozen and A. Roig-Alsina, on *Opuntia* sp. (2♀ 2♂♂ AMNH). Payogasta, January 1991, M. Fritz (25♂ AMNH). **Santiago del Estero:** El Pinto, November 1956 (1♀ CUIIC). Choya, January 1958 (11♀ 9♂ 13♂ SEMC). **Tucumán:** Amaichá del Valle, 23 November 1989, J. G. Rozen and A. Roig-Alsina, on *Opuntia* sp. (1♂ AMNH). Amaichá del Valle, 2 November 1989, J. G. Rozen and A. Roig-Alsina (2♂♂ AMNH). 7–11 km E-SE Amaichá del Valle, 23 November 1993, J. G. Rozen (1♂ AMNH).

Floral records.—This species has been captured at flowers of *Echinopsis leucantha*, *Gymnocalycium* sp., *Opuntia glomerata*, *O. quimilo*, *O. sulphurea*, *Trichocereus candicans*, *T. terscheckii* (new records). A single male of *A. ochracea* has been captured consuming nectar of the composite *Senecio flagellisetis*.

Phenology.—*Arhysosage ochracea* has been captured from late October through late February.

Comments.—Moure (1958: 45) mentions that the type of *C. castellani* is located in the USNM. Actually, the USNM specimen is a paratype while the holotype of Cockerell's species is housed in the AMNH. This is the most common species of the genus and the most variable in size. Smaller individuals of this species were previously known under the name *A. germana* and before that as *Camptopoeum castellani*.

An attempt to locate the type of *A. johnsoni* was unsuccessful. It was at one time in the collection in Buenos Aires but is now missing. It was at one time in the possession of Moure and as it may still be with him, I have hesitated to designate a



Figs. 9–10. *Arhysosage atrolunata* n. sp., faces, pubescence omitted. 9, Female. 10, Male, ff = facial fovea. Stippling indicates black areas, remainder yellow.

neotype. I have followed Moure (1958) in considering *A. johnsoni* to be a synonym of *A. ochracea*.

***Arhysosage atrolunata* Engel, new species**

(Figs. 9–10, 29, 35, 41, 45)

Diagnosis.—The males of this species can be immediately distinguished by the black, crescent-shaped marking around the ocelli in males (Fig. 10), the predominantly black mesoscutum, and nearly uniformly colored metasoma, which is amber to dark brown with yellow spots laterally on T1–2. Females of *A. atrolunata* lack metasomal banding, possess round punctures on the clypeus, and have dense setal tufts on the apicolateral margins of the clypeus.

Description.—As for *A. ochracea* (see below) with the following modifications: **Male:** Total body length 9.4–11.4 mm; forewing length 5.8–6.5 mm. Head width 3.1–3.7 mm, length 2.2–2.6 mm. Mandible longer than compound eye; inner tooth well-defined and somewhat rounded (Fig. 10). Upper interorbital distance 1.7–2.1

mm, lower interorbital distance 2.0–2.7 mm. Intertegular distance 2.0–2.6 mm. Basitibial plate apex broadly rounded. Terminalia as depicted in figures 29, 35, 41, and 45.

Head mostly yellow except facial foveae black, two spots on clypeus dark brown to black, and large crescent-shaped black pattern connecting dorsal margins of facial foveae and running across and just posterior to ocelli (Fig. 10). Pronotum yellow except mediotransverse band of dark brown to black running onto lateral surface and lower lateral border. Mesoscutum yellow with three longitudinal stripes of black, stripes very broad so that yellow areas quite narrow. Scutellum yellow except lateral three-quarters of axilla dark brown to black. Metanotum yellow. Pleura dark brown to black except hypoepimeral area, metepisternum, and upper corner of preepisternal area yellow. Procoxa and protrochanter dark brown to black; profemur dark brown to black except yellow on outer surface and in a longitudinal band on inner surface; remainder of foreleg yellow; mesocoxa and me-

sotrochanter dark brown to black; ventral border of mesotibia dark brown to black; remainder of midleg yellow; metacoxa and metatrochanter dark brown to black; metafemur dark brown to black except apex yellow; remainder of hind leg amber. Propodeum yellow except basally bordering metanotum black with mediolongitudinal, broad line of black running from the basal area onto posterior surface and bordering ventral margins of posterior surface. Mediolongitudinal line of T1 anterior surface amber, remainder amber or light brown except transverse band of yellow before apical border, band interrupted medially by amber coloration; T2 amber with lateral spots of yellow; remaining terga brown to black; sterna amber to dark brown.

Terga with sparse hairs except lateral to pygidial plate where they are long, dense, frequently branched, and amber; sterna similar except patches of long, amber hairs on either side of apical cleft of S6.

Female: As described for the male except as indicated: Total body length 9.4 mm; forewing length 5.7 mm. Head width 3 mm, length 2.2 mm. Upper interorbital distance 1.6 mm, lower interorbital distance 1.8 mm. Intertegular distance 1.8 mm.

Facial coloration as in figure 9. Proboscis light brown; labrum, hypostomal fossa, postgena, and preoccipital area dark brown. Antenna brown. Pronotum dark brown except pronotal lobe, median basal border, and median apical border yellow. Mesoscutum black except two narrow longitudinal stripes on either side of median line and border with tegula yellow. Scutellum yellow except basal border and central disc black; axilla black. Metanotum and tegula yellow. Pleura black except metepisternum yellow. Legs dark brown except apices of pro- and mesofemur, entirety of pro- and mesotibiae, and entirety of pro- and mesotarsi yellow. Metasoma uniformly amber.

Holotype.—ARGENTINA: **Cordoba:** ♂, W. M. Davis (LACM). **Allotype.**—ARGEN-

TINA: **Cordoba:** ♀, [W. M.] Davis (LACM). **Paratypes.**—ARGENTINA: **Cordoba:** W. M. Davis (1♂ LACM). **Salta:** Rosario de Lerma, El Golgota, 2400 m, 21 January 1986, J. L. Neff, on *Opuntia* sp. (2♂♂ AMNH, 1♂ CTMI).

Additional material.—ARGENTINA: **Salta:** Payogasta, January 1991, M. Fritz (1♂ AMNH).

Floral records.—*Arhysosage atrolunata* has been captured on flowers of an unidentified *Opuntia*.

Etymology.—The specific epithet is derived from the Latin words *ater* (black) and *lunatus* (crescent-shaped) and refers to the black, crescent moon-shaped marking on the vertex of males just behind the ocelli.

Phenology.—This species has presently only been captured in January.

Comments.—The crescent shaped pattern on the face of the males can be easily confused with a similar pattern that occurs in females of *A. flava*. Males of *A. flava*, however, have the face completely yellow except for the facial foveae, which are black in all species. Since females of *A. atrolunata* lack metasomal banding whatsoever, they therefore superficially resemble females of *A. flava*. Females of *A. atrolunata* differ from those of *A. flava* in their facial pattern, in having round punctures on the clypeus, and in possessing dense setal tufts on the apicolateral margins of the clypeus.

Arhysosage bifasciata (Fries), new combination

(Figs. 11–12, 30, 36, 42, 47)

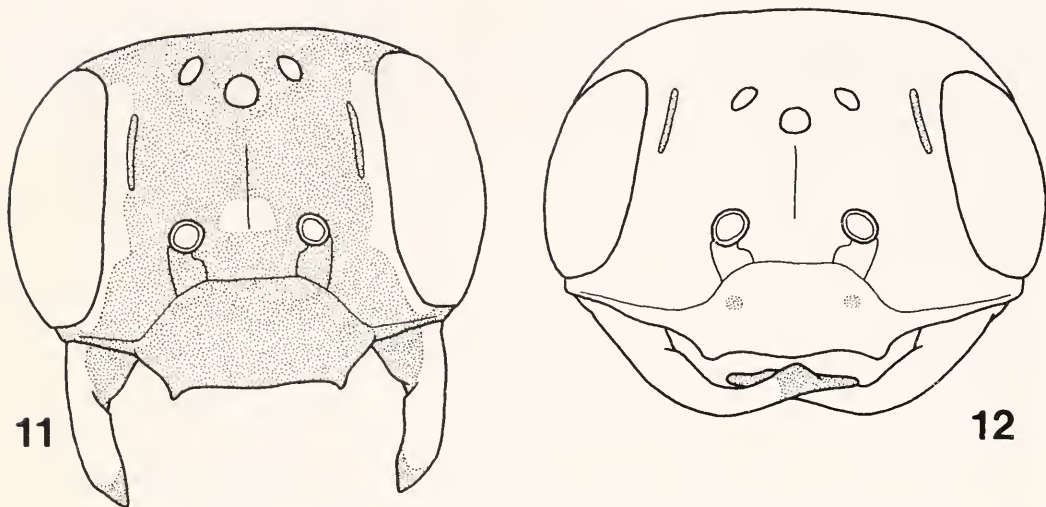
Psathyria bifasciata Fries 1908: 41. Examined (ZMHB).

Camptopoeum bifasciatum (Fries); Jörgensen 1912: 118.

Camptopoeum opuntiarum Jörgensen 1912: 118. Examined (MLPA). **New synonymy.**

Ruiziella bifasciata (Fries); Timberlake 1952a: 105.

Diagnosis.—Females of *A. bifasciata* are distinctive for their dark coloration with only a few yellow markings; the propo-



Figs. 11–12. *Arhysosage bifasciata* (Fries), faces, pubescence omitted. 11, Female. 12, Male. Stippling indicates black areas, remainder yellow.

deum is entirely black or infrequently marked by tiny yellow spots on the posterior border of the basal area. Males of *A. bifasciata* differ from *A. ochracea* in the absence of banding on the metasoma and in the terminalia.

Description.—As for *A. ochracea* (see below) with the following modifications: **Male:** Total body length 10.5–11.3 mm; forewing length 6.7–7.0 mm. Head width 3.3–3.7 mm, length 2.4–2.6 mm. Mandible longer than compound eye; inner tooth weak (Fig. 12). Upper interorbital distance 1.9–2.2 mm, lower interorbital distance 2.4–2.6 mm. Intertegular distance 2.0–2.2 mm. Basitibial plate apex broadly rounded. Terminalia as depicted in figures 30, 36, 42, and 47.

Proboscis light brown; hypostomal fossa as well as bordering areas of postgena and preoccipital area yellow to amber. Preepisternum, mesepisternum, and metepisternum yellow or amber; propleuron amber. Legs amber; claws reddish brown at apices; mesotibial spine and metatibial spurs amber. Propodeum yellow except basally bordering metanotum dark brown with a mediolongitudinal, narrow line of brown running from the basal area onto

the posterior surface and ending medially at marginal area of propodeum. Metasoma uniformly amber.

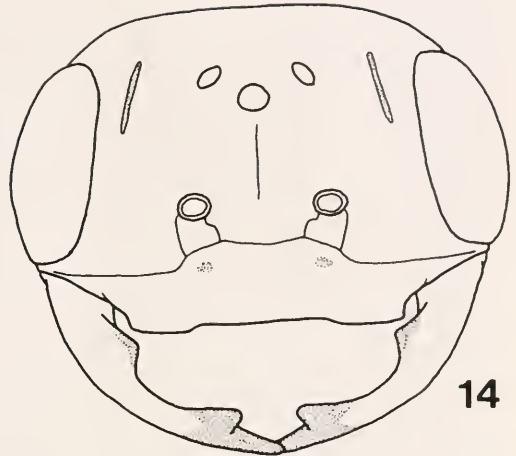
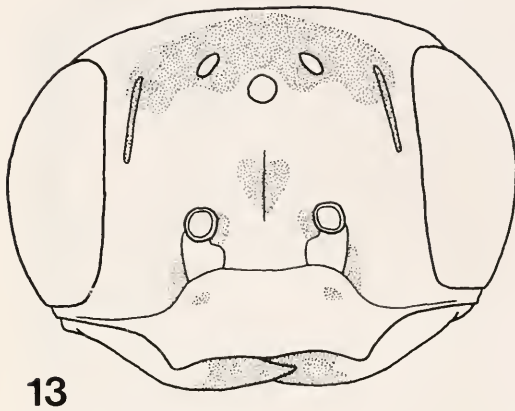
Female: As described for the male except as indicated: Total body length 9.3–10.9 mm; forewing length 5.2–6.1 mm. Head width 2.5–3.0 mm, length 2.0–2.6 mm. Upper interorbital distance 1.5–1.9 mm, lower interorbital distance 1.7–2.2 mm. Intertegular distance 1.6–2.0 mm.

Facial color pattern as in figure 11; remainder of head black except gena yellow. Mesosoma black except yellow on pronotal lobe, apicolateral corner of pronotal dorsal surface, tegula, posterior margin of scutellum, and pro- and mesofemur-tibia junctions. Metasoma black except apical margins of terga dark brown; T1–2 with small lateral spots of yellow just inside graduli; T3 with similar spots but lengthened transversely; T4–5 with narrow median bands of yellow.

Pubescence of legs and metasoma fuscous.

Holotype.—ARGENTINA: **Mendoza:** ♀, [no date or collector's name] (ZMHB).

Additional material.—ARGENTINA: **Mendoza:** 24 November 1905, Jensen (1♀ ZMHB). Cerrillos sur C. de la Gloria, December 1976, A. Roig-Alsina



Figs. 13–14. *Arhysosage flava* Moure, faces, pubescence omitted. 13, Female. 14, Male. Stippling indicates black areas, remainder yellow.

(1♀1♂MACN). [no locality information, #5a] (1♂MACN). 16 November 1906, P. Jörgensen (1♀MLPA: holotype of *C. opuntiarum*). 15 km W. Mendoza, 1000 m, 7–8 December 1979, C. and M. Vardy, B.M. 1980–67, on *Trichocereus candicans* or *Opuntia sulphurea* (2♀4♂BMNH). 1200 m, 3 November 1908 (1♀AMNH). 5 km N. San Rafael, 20 November 1973, J. L. Neff, on *Opuntia sulphurea* (1♀CTMI). Catamarca: El Desmonte, 23–24 November 1989, J. G. Rozen and A. Roig-Alsina, nests 1–3, 5–6 (8♀♀AMNH). El Desmonte, 25 November 1993, J. G. Rozen (1♀AMNH). El Desmonte, 1 December 1989, J. G. Rozen and A. Roig-Alsina, on *Opuntia* sp. (1♀AMNH). El Desmonte, 7 November 1989, J. G. Rozen and A. Roig-Alsina, nest 1 (1♀AMNH). Punta de Balasto, 2 November 1989, J. G. Rozen and A. Roig-Alsina, on *Opuntia* sp. (1♀AMNH). Santa Maria, 18 January 1973, J. L. Neff, on *Opuntia sulphurea* (1♀CTMI). Salta: Rosario de Lerma, El Golgota, 2400 m, 21 January 1986, J. L. Neff, on *Opuntia* sp. (1♀CTMI). Payogasta, January 1991, M. Fritz (13♀♀10♂♂AMNH). Tastli, 3000 m, January 1991, M. Fritz (1♀AMNH). El Allsal, January 1994, M. Fritz (1♀AMNH).

Floral records.—This species has been captured at flowers of *Opuntia* sp. and *Echinocactus* sp. (Jensen-Haarup 1908: as *Psaenythia bifasciata*) as well as *Trichocereus candicans* and *O. sulphurea* (new records).

Phenology.—*Arhysosage bifasciata* has been captured from early November through late January.

Comments.—As mentioned in the diagnosis of the species, females of *A. bifasciata*

are distinctive for their dark coloration. Most of the body is black with only a few yellow markings on the face (Fig. 11), mesosoma, and metasoma. This characteristic easily separates females of *A. bifasciata* from all other species, only infrequently being confused with darker females of *A. ochracea*. In these later cases, however, females of *A. ochracea* are always still much more yellow and the propodeum in particular is mostly yellow with black restricted to the basal margin and in a median band while in *A. bifasciata* the propodeum is entirely black or infrequently marked by tiny yellow spots on the posterior border of the basal area.

***Arhysosage flava* Moure**
(Figs. 13–16, 28, 34, 40, 48)

Arhysosage flava Moure 1958: 45. Examined (SEMC).

Diagnosis.—This species is notable for the absence of metasomal bands, the elongate punctures of the clypeus (Figs. 15–16), the absence of dense setae on the lateral borders of the clypeus, and the patterning of black marks on the female face (Fig. 13).

Description.—As for *A. ochracea* (see below) with the following modifications:



Male: Total body length 7.8–10.4 mm; forewing length 4.8–6.6 mm. Head width 2.4–3.7 mm, length 1.6–2.4 mm. Mandible longer than compound eye; inner tooth strong, somewhat rounded although frequently pointed (Figs. 14–15). Upper interorbital distance 1.5–2.4 mm, lower interorbital distance 1.6–2.8 mm. Intertegular distance 1.5–2.2 mm. Basitibial plate apex broadly rounded. Terminalia as depicted in figures 28, 34, 40, and 48.

Outer interspace of mandible with fine longitudinal striae at level of inner tooth. Clypeus with faint, coarse punctures, punctures nearly contiguous and longitudinally extended making surface appear roughened. Supraclypeal area with coarse, nearly contiguous punctures. Face lateral to outer subantennal sutures and below level of antennal sockets with punctures separated by 1–2 times puncture width, integument otherwise smooth; at level of antennal sockets punctures become smaller, well-defined, and gradually more closely spaced until nearly contiguous at level just above antennal sockets. Gena as on vertex except punctures becoming faint on lower three-quarters and separated by 2–4 times puncture width, integument otherwise smooth, punctures also become fainter posteriorly near preoccipital area. Postgena faintly and coarsely punctured, integument between punctures smooth.

Proboscis light brown to yellow; hypostomal fossa as well as bordering areas of postgena and preoccipital area yellow. Preëpisternum, mesepisternum, metepisternum, and propleuron yellow. Legs yellow. Propodeum yellow except sometimes with dark brown to black spot medially on basal area. Mediolongitudinal line of T1 anterior surface yellow; terga and ster-

na uniformly yellow or yellowish-amber, sometimes with light brown spot on T2 outside of lateral gradulus (on ventral-facing surface of tergum).

Pubescence along apicolateral margins of clypeus sparse and simple. Terga with sparse hairs except lateral to pygidial plate where they are long, dense, frequently branched, and golden or amber; sterna similar without patches of long, golden hairs on either side of apical cleft of S6, hairs golden, short, and not clustered into patches.

Female: As described for the male except as indicated: Total body length 8.0–10.6 mm; forewing length 4.8–6.3 mm. Head width 2.3–3.0 mm, length 1.7–2.4 mm. Upper interorbital distance 1.4–2.0 mm, lower interorbital distance 1.5–2.2 mm. Intertegular distance 1.5–2.0 mm.

Face colored as in figure 13. Gena yellow. Proboscis dark brown; hypostomal fossa as well as bordering areas of postgena and preoccipital area dark brown to black. Labrum yellow. Scape outer surface yellow, inner surface black; remainder of antenna light brown. Pronotum yellow except transverse median line of dark brown to black on dorsal surface. Mesoscutum yellow except three very narrow longitudinal stripes and border with tegula black. Scutellum yellow except anterior margin black. Tegula and metanotum yellow. Pleura yellow except ventrally dark brown to black; propleuron black. Wing veins amber. Coxae and trochanters black; femora black basally, remainder yellow; remainder of legs yellow. Propodeum yellow with basal margin and narrow mediolongitudinal line black. Terga yellow; sterna yellow with paired spots of brown on central discs.

Figs. 15–16. Scanning electron micrographs of *Arhysosage flava* Moure, male head. 15, Full face; the mandibular striations are slightly visible on the outer border of the left mandible (right side in the micrograph). 16, Labrum and lower half of face; note the sharply curved inner subantennal suture and the position of the anterior tentorial pit nearly at the midpoint of the outer subantennal suture.

Pubescence along apicolateral margins of clypeus sparse and simple. Terga with sparse hairs except lateral to pygidial plate where they are long, dense, frequently branched, and amber; sterna similar with scattered short, amber hairs.

Variation.—The areas of dark brown to black on the venter of the female can sometimes be light brown or with various regions being entirely yellow. Similarly, T1 in the female can sometimes have a small brown spot centrally by the bend separating the anterior-facing and dorsal-facing surfaces. On the face, females sometimes have small black patches at the upper border of the compound eyes. These patches can sometimes connect the black crescent of the upper face with the compound eye margins.

Holotype.—ARGENTINA: **Formosa:** ♂, Ing. Juarez, December 1950, F. H. Walz (SEMC).

Additional material.—ARGENTINA: **Catamarca:** Recreo, December 1951, F. H. Walz (1♀ USNM, 1♂ AMNH, 1♀3♂ SEMC). **Cordoba:** Jesus Maria, 3 December 1973, J. L. Neff, on *Opuntia* sp. (1♀6♂ CTMI). Arguello, J. A. de Carlo and M. J. Viana (1♀ SEMC). **Formosa:** Ing. G. N. Juarez, 30 November 1949, F. Monrós (1♀1♂ MACN). Ing. Juarez, December 1950, F. H. Walz (1♂ AMNH, 1♂ BMNH, 1♀3♂ SEMC). Gran Guardia, 15 November 1952, J. Foerster (1♀1♂ SEMC). **San Luis:** A. Stevenin (3♂♂ MACN). **Santiago del Estero:** Rio Salado, Wagner (1♀2♂♂ MACN). [no date or collector's name] (2♀♀3♂♂ MACN). El Pinto, November 1956 (25♀♀25♂♂ SEMC). Choya, January 1958 (4♀♀17♂♂ SEMC). M. Gomez (1♀1♂ SEMC). Dpto. Matará, Desvio 511, 24 October 1928, M. Gomez (2♂♂ SEMC). Loreto, December 1992, M. Fritz (1♀ AMNH). **Salta:** Cruz Quemada, 40 km S General Guemes, 20 November 1989, J. G. Rozen and A. Roig-Alsina (2♀♀21♂♂ AMNH). Same as previous collection data except in copula on flowers of *Opuntia* sp. (1♀1♂ AMNH). Same as previous [♀♂ on same pin] (1♀1♂ AMNH). Cruz Quemada, 31 km S General Guemes, 10 November 1989, J. G. Rozen and A. Roig-Alsina, on *Opuntia* sp. (3♀♀7♂♂ AMNH). Cruz Quemada, 9 November 1993, J. G. and B. L. Rozen, on *Opuntia* sp. (1♂ AMNH). 20 km W-NW Hickmann, 12–14 November 1989, J. G. Rozen and A. Roig-Alsina (1♀2♂♂ AMNH). **Santa Cruz:** San Isidro (1♂ AMNH). **PARAGUAY:** Chaco, Loma Plata, Arriagado, February 1993 (1♂ AMNH).

Floral records.—This species has at present been found only on flowers of an unidentified *Opuntia* (new record).

Phenology.—*Arhysosage flava* has been captured from early November into early February.

Comments.—This species resembles to some degree *A. ochracea* but differs most notably in the absence of metasomal bands, the elongate punctures of the clypeus (Figs. 15–16), the absence of dense setae on the lateral borders of the clypeus, and the patterning of black marks on the female face (Fig. 13). *Arhysosage flava* is most similar to the poorly known *A. zamicro* but differs in the male mandible being longer than the compound eye (Fig. 14), the absence of black markings on the mesepisterna, the presence of fine striae on the mandibular outer interspace (Fig. 15), and the broadly rounded basitibial plate apex (Fig. 8).

The above specimens of this species in Bolivia and Paraguay are the first records for this genus in both countries.

***Arhysosage zamicro* Engel, new species**
(Figs. 22, 27, 33, 39, 46)

Diagnosis.—This is presently distinguished by the combination of the absence of banding on the metasoma, the elongate punctures of the clypeus, the mandible being slightly shorter in length than the length of the compound eye, the absence of mandibular striae, the presence of ventral-facing black spots on the mesepisterna, and the pointed apex of the basitibial plate (Fig. 7).

Description.—As for *A. ochracea* (see above) with the following modifications: **Male:** Total body length 6.8 mm; forewing length 4.2 mm. Head width 2 mm, length 1.3 mm. Mandible shorter than compound eye; inner tooth strong and pointed (Fig. 22). Upper interorbital distance 1.2 mm, lower interorbital distance 1.4 mm. Inter-ocular distance 1.3 mm. Basitibial plate apex pointed (similar to that depicted for

A. cactorum: Fig. 7). Terminalia as depicted in figures 27, 33, 39, and 46.

Outer interspace of mandible with faint, coarse punctures, integument between faintly imbricate, without striae. Clypeus with faint, coarse punctures, punctures nearly contiguous and longitudinally extended making surface appear roughened (as in *A. flava*). Supraclypeal area with coarse, nearly contiguous punctures. Face outside of outer subantennal sutures and below level of antennal sockets with punctures separated by 1–2 times puncture width, integument otherwise smooth; at level of antennal sockets punctures becoming smaller, well-defined, and gradually more closely spaced until nearly contiguous just above antennal sockets. Gena as on vertex except punctures becoming faint on lower half and separated by 2–3 times puncture width, integument otherwise smooth, punctures become faint near preoccipital area. Postgena faintly imbricate.

Head mostly yellow except facial foveae black and two spots on clypeus dark brown. Inner tooth and mandibular apex reddish brown to black. Proboscis light brown; hypostomal fossa as well as bordering areas of postgena and preoccipital area yellow. Antenna yellow. Mesosoma yellow except posterior third of axilla black and spot of dark brown on ventral-facing surface of mesepisternum. Metasoma yellow except small dark brown spot laterally outside of gradulus on T2.

Pubescence along apicolateral margins of clypeus sparse and simple. Terga with sparse hairs except lateral to pygidial plate where they are long, dense, frequently branched, and golden; sterna similar without patches of long, golden hairs on either side of apical cleft of S6, hairs golden, short, and not clustered into patches.

Female: Unknown.

Holotype.—ARGENTINA: **Santiago del Estero:** ♂, El Pinto, November 1956 (SEMC).

Etymology.—The specific epithet is a

combination of the Greek words *za* (very) and *mikros* (small).

Phenology.—This species has so far only been captured in November.

Comments.—This is presently the smallest known species of *Arhysosage*. It is similar to smaller specimens of *A. ochracea* but differs most notably in the absence of the banding pattern on the metasoma, in this respect resembling *A. flava* to which it is perhaps a close relative. Like *A. flava*, *A. zamicro* has the elongate punctures of the clypeus but differs from this species in the mandible being slightly shorter than the compound eye, the absence of mandibular striae, the presence of ventral-facing black spots on the mesepisterna, and the pointed apex of the basitibial plate (Fig. 7).

Arhysosage cactorum Moure

(Figs. 4, 6–7, 23–25, 31, 37, 43–44)

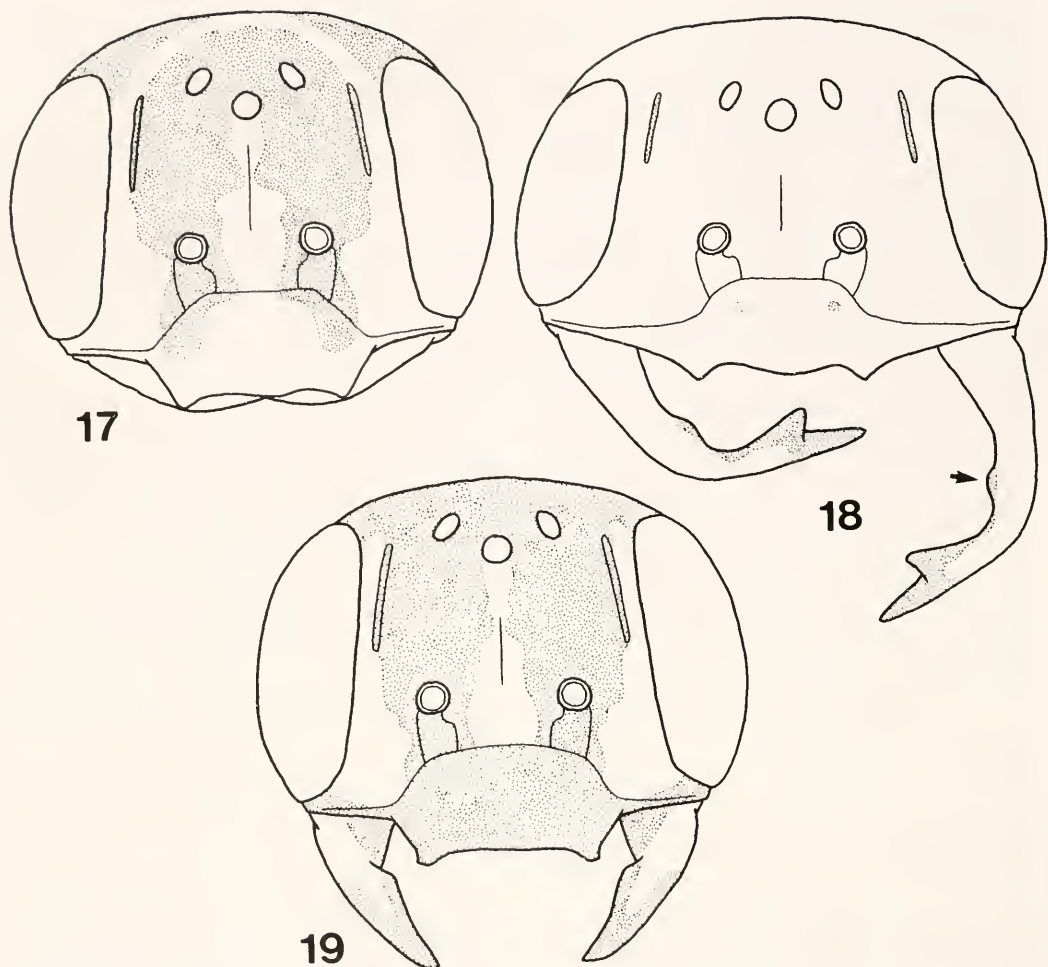
Arhysosage melanotricha Schlindwein and Wittmann 1995: 32. *Lapsus calami* and *nomen nudum*.

Arhysosage cactorum Moure 1999: 241

Arhysosage melanotricha Moure 1999: 245. **New synonymy.**

Diagnosis.—The male of this species is recognized by the upper half of the face being black (Figs. 24–25), the absence of an emargination at the pygidial plate apex (Fig. 4), the apices of penis valves not bending ventrally (Fig. 44), and the aedeagus not extending apically near to the apices of the penis valves (Figs. 43–44). The female can be distinguished by the mostly yellow labrum, the absence of yellow markings of any sort on the metasoma, and the pygidial plate strongly curved ventrally towards apex in profile and dorsally quickly tapering to a well-defined point.

Description.—As for *A. ochracea* with the following modifications and additions: **Male:** Total body length 8.8 mm; forewing length 5.7 mm. Head width 3 mm, length 2 mm. Mandible longer than compound eye; inner tooth strong and pointed (Figs. 24–25). Upper interorbital distance 1.8



Figs. 17–19. *Arhysosage ochracea* (Friese), faces, pubescence omitted. 17, Female, most common color pattern. 18, Male, arrow indicates inner tooth. 19, Female, second facial pattern. Stippling indicates black areas, remainder yellow.

mm, lower interorbital distance 2 mm. Intertegular distance 1.8 mm. Basitibial plate apex pointed (Fig. 7). Apex of pygidial plate not emarginate (Fig. 4). Apex of penis valve not bending ventrally (Fig. 44); aedeagus not extend apically near to apex of penis valve (Figs. 43–44); terminalia otherwise as depicted in figures 31, 37, and 43–44.

Integument of mandible in outer interspace roughened, becoming smooth by point where outer ridge and condylar ridge meet. Clypeus with faint, coarse punctures, punctures nearly contiguous

and longitudinally extended making surface appear roughened. Subantennal areas faintly imbricate. Supraclypeal area below antennal sockets and between inner subantennal sutures minutely roughened; between antennal sockets punctures well-defined, smaller, and nearly contiguous. Face outside of outer subantennal sutures and below level of antennal sockets coarsely punctured, punctures separated by puncture width or less, integument between smooth; at level of antennal sockets punctures become smaller, well-defined, and gradually more closely spaced until



Figs. 20-21. Scanning electron micrographs of *Arhysosage ochracea* (Fries), male head. 20, Full face. 21, Labrum, lower paraocular area, and supraclypeal area.

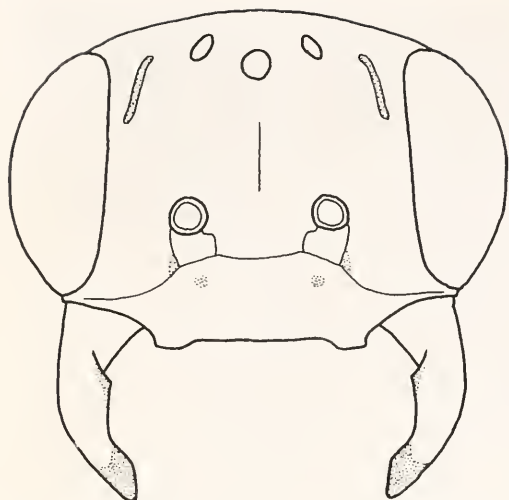
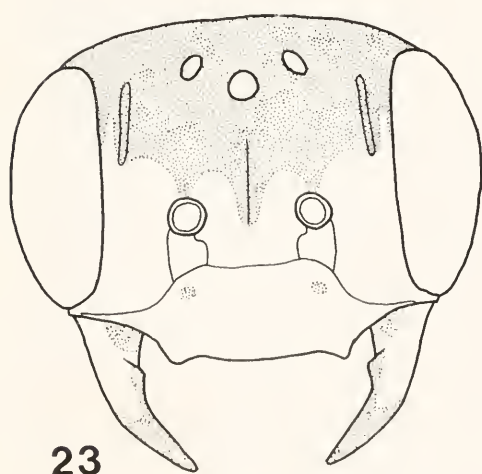


Fig. 22. *Arhysosage zamira* n. sp., male face, pubescence omitted. Stippling indicates black areas, remainder yellow.

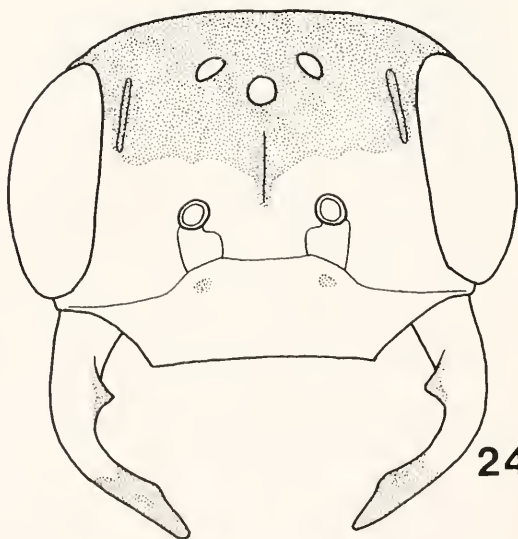
nearly contiguous by level just above antennal sockets; remainder of face and vertex with such fine, well-defined punctures, nearly contiguous. Gena as on vertex except punctures becoming smaller and faint. Pronotal lateral surfaces imbricate and impunctate. Tegula imbricate. Metanotum with contiguous faint, coarse, punctures, integument between imbricate.

Preëpisternal area as on mesoscutum except punctures becoming faint and slightly more widely spaced ventrally; mesepisternum with faint, coarse punctures separated by less than puncture width, integument between faintly imbricate, punctures become fainter ventrally; metepisternum with faint, minute punctures separated by width or less, integument between imbricate. Propodeal lateral surface with minute, well-defined punctures separated by puncture width or less, integument between smooth; posterior surface as on lateral surface except punctures faint.

Head coloration as in figures 24–25. Proboscis brown; hypostomal fossa, postgena, and preoccipital area black. Labrum yellow. Scape with inner surface black, outer surface yellow; remainder of antenna brown. Pronotum black except pronotal lobe, medioapical border, and lateral spot yellow. Mesoscutum black except border with tegula and two very small spots bordering median line yellow. Scutellum yellow except mediobasal border black. Tegula and metanotum yellow. Pleura black



23



24

Figs. 23–24. *Arhysosage cactorum* Moure, faces, pubescence omitted. 23, Female. 24, Male. Stippling indicates black areas, remainder yellow.

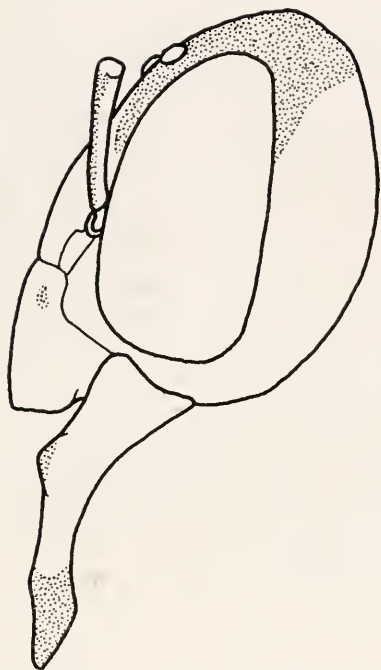
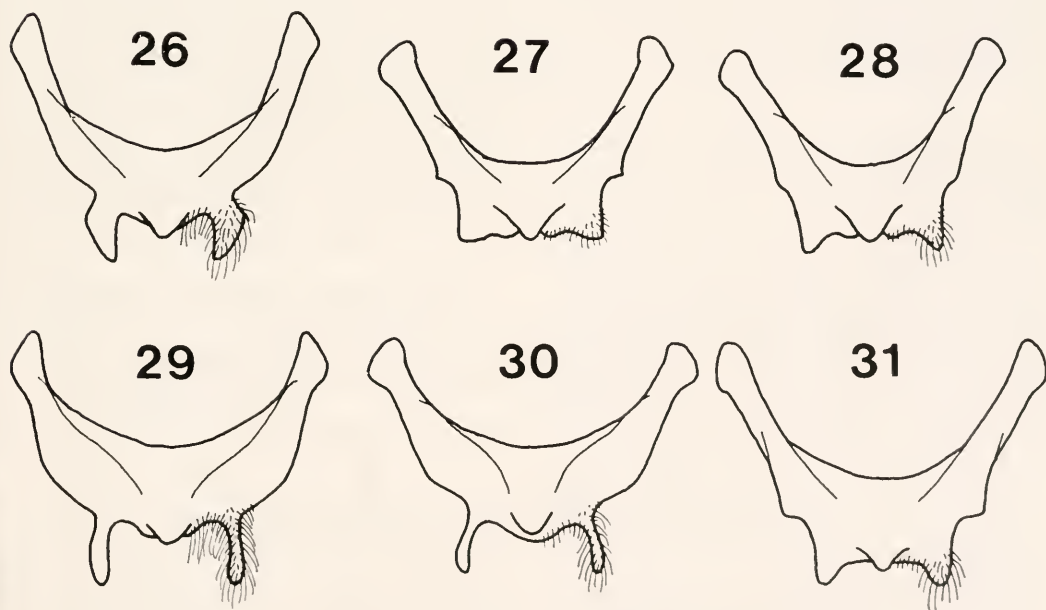


Fig. 25. *Arhysosage cactorum* Moure, lateral view of male head.

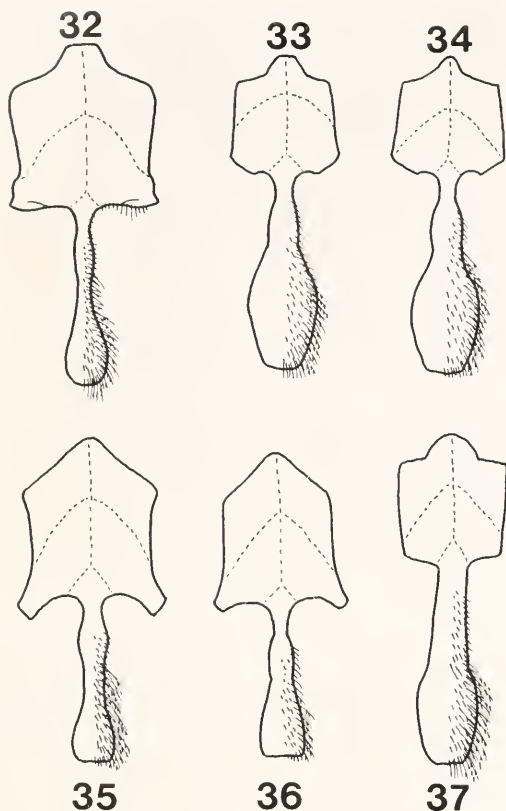
except upper quarter of preepisternal area and medial third of metepisternum yellow. Coxae and trochanters black; basal border and inner surfaces of femora black, remainder yellow; remainder of legs yellow. Propodeum yellow except basally bordering metanotum black with a medio-longitudinal, narrow line of black running from the basal area onto the posterior surface and ending medially at marginal area of propodeum; basal half of lateral surface black. Metasoma uniformly amber.

Pubescence along apicolateral margins of clypeus sparse and simple. Terga with sparse hairs except lateral to pygidial plate where they are long, dense, frequently branched, and amber; sternal hairs amber, short, and not clustered into patches.

Female: As described for the male except as indicated: Total body length 8.3 mm; forewing length 5.9 mm. Head width 2.9 mm, length 1.9 mm. Upper interorbital distance 1.7 mm, lower interorbital distance 1.8 mm. Intertegular distance 1.8 mm. Pygidial plate in profile strongly



Figs. 26–31. Male S7 of *Arhysosage* species, pubescence on right halves only. 26, *Arhysosage ochracea* (Friese). 27, *A. zamica* n. sp. 28, *A. flava* Moure. 29, *A. atrolunata* n. sp. 30, *A. bifasciata* (Friese). 31, *A. cactorum* Moure.



Figs. 32–37. Male S8 of *Arhysosage* species, pubescence on right halves only. 32, *Arhysosage ochracea* (Fries). 33, *A. zamica* n. sp. 34, *A. flava* Moure. 35, *A. atrolunata* n. sp. 36, *A. bifasciata* (Fries). 37, *A. cactorum* Moure.

curved ventrally towards apex, quickly tapering to well-defined point in dorsal view.

Facial coloration as in figure 23. Gena yellow. Proboscis dark brown; hypostomal fossa, postgena, and preoccipital area dark brown. Labrum yellow except apical margin brown. Pronotum black except

pronotal lobe, posterior median border, and anterior median border yellow. Mesoscutum black except border with tegula yellow. Tegula yellow. Axilla and anterior half of scutellum black, remainder yellow. Metanotum yellow except anterior border black. Pleura black. Legs dark brown except apices of pro- and meso-femora, outer surface of protibia, inner surface of mesotibia, and protarsus yellow. Basal area of propodeum yellow except basal margin and mediolongitudinal line black; lateral and posterior surfaces black except two yellow spots on either side of propodeal pit yellow. Terga amber except anterior-facing surface of T1 dark brown, median band of dark brown on T2, and apical half of T6; sterna light brown.

Topotype.—BRAZIL: **Rio Grande do Sul:** ♂ Lavras do sul ("Rincão do Inferno") 11 January 1991, C. Schlindwein. I was unable to examine the holotype but have seen a male and female of Moure's species (identified by Padre Moure) in the collection of Isabel Alves dos Santos. The male I examined was collected at the same time and place as the holotype.

Additional material.—ARGENTINA: **Salta:** El Carril, 11 November 1989, J. G. Rozen and A. Roig-Alsina, on *Opuntia* sp. (♂ AMNH). N. El Carril, 13 November 1993, J. G. and B. L. Rozen, on *Opuntia* sp. (♀ AMNH). Sumalao, November 1994, M. Fritz (4♀ 3♂ AMNH). BRAZIL: **Rio Grande do Sul:** Lavras do sul ("Rincão do Inferno") 11 January 1991, C. Schlindwein. (♂ PCIA). Caçapava do Sul, 11 November 1990, C. Schlindwein (♀ PCIA).

Floral records.—Captured at flowers of an unidentified *Opuntia*.

Phenology.—This species has been collected in November and January.

KEY TO SPECIES OF ARHYSOSAGE

(Unknown and not included: Females of *A. zamica*)

- | | |
|--|---|
| 1. Males. | 2 |
| – Females. | 7 |
| 2. Face predominantly yellow (Figs. 10, 12, 14, 18, 22); scape yellow or at most with small brown patches on inner surface; pygidial plate apex emarginate, sometimes weakly so (Fig. 5); apex of penis valve bent ventrally (Figs. 45–49). | 3 |

- Upper half of face entirely black (Fig. 24); scape yellow on outer surface, black on inner surface; pygidial plate apex not emarginate (Fig. 4); apex of penis valve not bent ventrally (Fig. 44). *A. cactorum* Moure
- 3. Face with black markings restricted to facial fovea (Figs. 12, 14, 18, 22). 4
- Face with black markings on facial fovea and with a black crescent-like area that connects foveae just above ocelli (Fig. 10). *A. atrolunata* n. sp.
- 4. Clypeus with coarse, elongate punctures (Fig. 16); clypeus with dense pubescence at apicolateral margins. 5
- Clypeus with coarse, rounded punctures (Fig. 21); clypeus with sparse pubescence at apicolateral margins. 6
- 5. Mandible longer than compound eye (Fig. 14), with fine striae on outer interspace (Fig. 15); mesepisterna yellow, without black markings; basitibial plate apex broadly rounded (Fig. 8). *A. flava* Moure
- Mandible slightly shorter than compound eye (Fig. 22), outer interspace without striae, instead imbricate with coarse punctures; mesepisterna with paired black spots; basitibial plate apex pointed (Fig. 7). *A. zamicra* n. sp.
- 6. Metasoma banded, yellow with transverse amber bands (Fig. 1). *A. ochracea* (Friesse)
- Metasoma uniformly amber. *A. bifasciata* (Friesse)
- 7. Labrum black or brown, infrequently with some small yellow spots or bands; pygidial plate straight or weakly curved in profile, dorsally gently tapering to narrowly rounded apex. 8
- Labrum mostly yellow except apical border brown; pygidial plate strongly curved in profile, dorsally quickly tapering to a well-defined point at apex. *A. cactorum* Moure
- 8. Clypeal integument with coarse, rounded punctures (Fig. 21), clypeus with some black markings aside from paired spots of brown (Figs. 9, 11, 17, 19). 9
- Clypeal integument with coarse, elongate punctures (Fig. 16), clypeus yellow without black markings aside from paired spots of brown (Fig. 13). *A. flava* Moure
- 9. Propodeum entirely black, infrequently with small paired spots or transverse bands of yellow along posterior border of basal area; facial color pattern as in figure 11; metasoma mostly black with small yellow spots or bands. *A. bifasciata* (Friesse)
- Propodeum yellow with black along anterior border of basal area and in a mediolongitudinal band running from border with metanotum to metasoma; facial color pattern as in figure 9, 17, or 19; metasoma frequently mostly yellow or amber, sometimes mostly dark but with complete transverse yellow bands on most segments. 10
- 10. Metasoma uniformly amber, without yellow banding or spots; facial color pattern as in figure 9. *A. atrolunata* n. sp.
- Metasoma banded; facial color pattern as in figure 17 or 19. *A. ochracea* (Friesse)

NOMINA NUDA IN ARHYSOSAGE

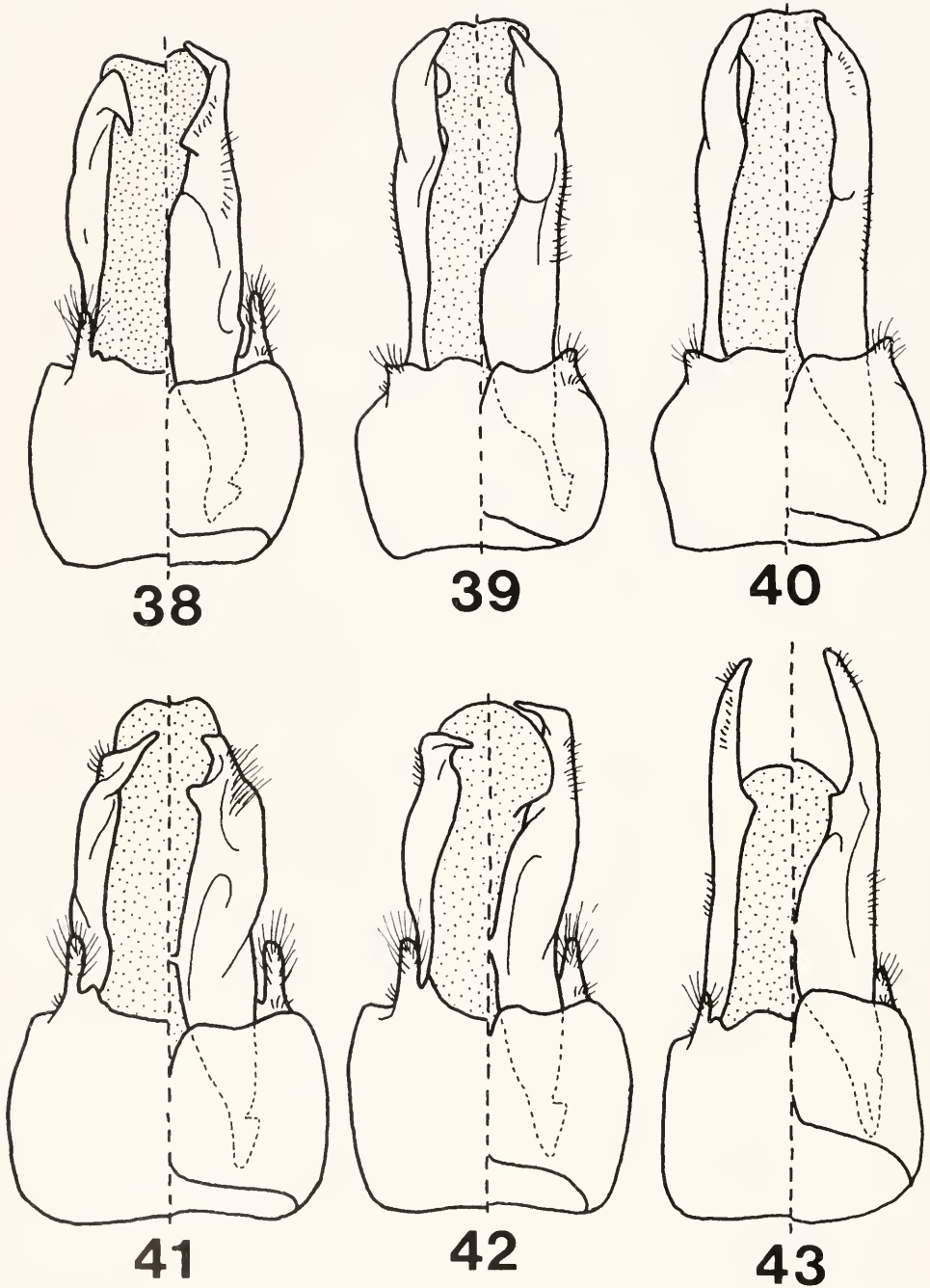
Arhysosage xanthina Moure, *nomen nudum*

Arhysosage xanthina Moure In Schlindwein and Wittmann 1995: 32.

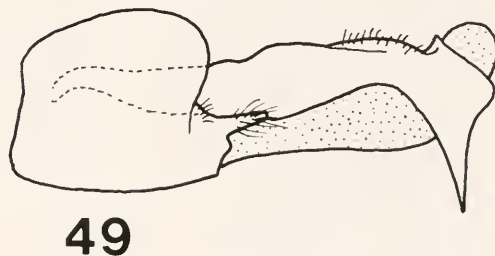
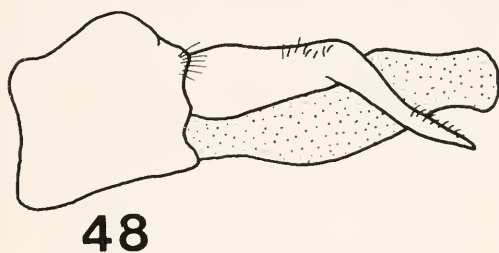
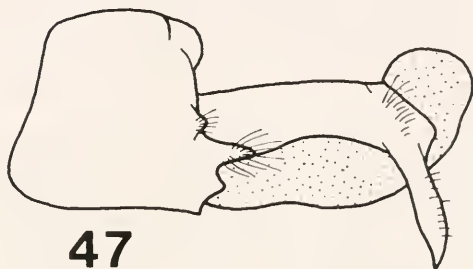
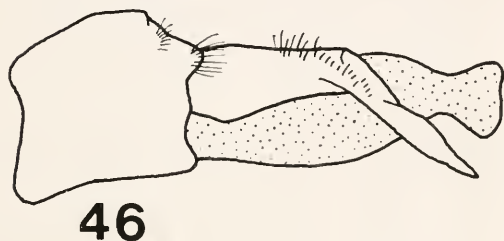
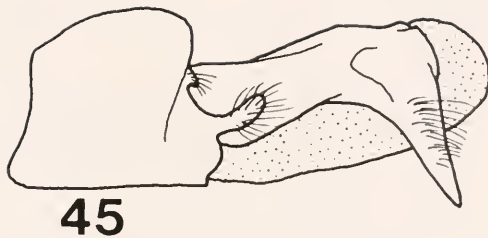
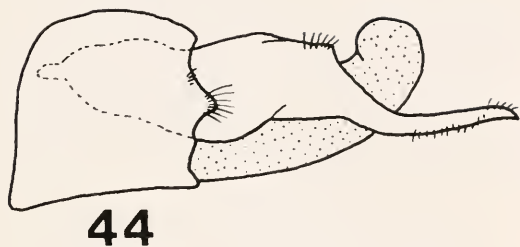
Comments.—Schlindwein and Wittmann (1995) presented a study on the pollination of the cactus genera *Notocactus* and *Gymnocalycium* in which they mention several species of *Arhysosage* visiting these flowers. Both in the text and in the ac-

knowledgments they attribute several *Arhysosage* identifications and names to Padre Moure.

The information presented in Schlindwein and Wittmann (1995) extends the range of the genus into southern-most Brazil. These authors record the locality at which they observed bees on cactus flowers as follows: Serra do Sudeste, southeast of Rio Grande do Sul (30°–32° S, 51°–54° W), Brazil, at approximately 500 m elevation. The area is described as subtropical to temperate being humid most of the year



Figs. 38–43. Male genitalia of *Arhysosage* species; left halves are ventral views, right halves are dorsal views. Aedeagus stippled in figures. 38, *Arhysosage ochracea* (Fries). 39, *A. zamica* n. sp. 40, *A. flava* Moure. 41, *A. atrolunata* n. sp. 42, *A. bifasciata* (Fries). 43, *cactorum* Moure.



Figs. 44–49. Male genitalia of *Arhysosage* species in lateral view; outlines of penis valve apodemes omitted except for a two species so as to contrast their shapes and demonstrate variation in the genus. Aedeagus stippled in figures. 44, *Arhysosage cactorum* Moure. 45, *Arhysosage atrolunata* n. sp. 46, *A. zamica* n. sp. 47, *A. bifasciata* (Friese). 48, *A. flava* Moure. 49, *A. ochracea* (Friese).

although with water deficiency from December through February. These authors also record bees visiting several cactus flowers: *Notocactus polyacanthus*, *N. succineus*, *N. sellowii*, *Gymnocalycium denudatum* (Schlindwein and Wittmann 1995) and *Frailea phaeodisca*, *F. pygmaea*, *N. neohorstii*, *N. ottonis*, *Opuntia brunneogemma*, *O. viridirubra* (Schlindwein 1995, Schlindwein and Wittmann 1997). On average 95% of the pollen in loads of individual females came from a single cactus species (Schlindwein and Wittmann op. cit.).

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I am grateful to Isabel Alves dos Santos for a loan of *A. cactorum* specimens and to Padre Jesús S. Moure

for communications concerning *Arhysosage*. I am thankful to the persons mentioned in the Materials and Methods who graciously loaned material under their stewardship. Molly G. Rightmyer kindly assisted with the scanning electron microscopy and preparation of the final images. I thank John L. Neff who provided information on floral associations for specimens of *Arhysosage* he collected during expeditions in 1972–1973 and 1986. John L. Neff, Molly G. Rightmyer, Jerome G. Rozen, Jr., and two anonymous reviewers read early versions of the manuscript and provided valuable suggestions for its improvement. Support for my studies has been generously provided by Robert G. Goelet, Chairman Emeritus of the AMNH Board of Trustees.

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NOTE

Cretobestiola, a replacement name for *Bestiola* Pulawski and Rasnitsyn, 1999 (Hymenoptera: Sphecidae)

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We recently described the sphecid wasp genus *Bestiola* (in Rasnitsyn *et al.* 1999) to accommodate four species from Lower Cretaceous of Spain, eastern Russia, and Mongolia. This generic name, however, is preoccupied by *Bestiola* Nikol'skaya (1963), an aphelinid, as pointed out to us by Mr. John K. Page (Zoological Records, York, Great Britain) and also by Signor Guido Pagliano (Torino, Italy). We therefore propose the name *Cretobestiola* to replace it. The name is derived from the Latin *creta* (chalk), with reference to Creta-

ceous geological period, and *bestiola* (little beast).

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NOTE

Two New Records of Pimpline Ichneumonids Attacking *Battus philenor* (Linnaeus) (Lepidoptera: Papilionidae)

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A series of seven ichneumonids rediscovered in the American Museum of Natural History collection offers two new host associations. All seven parasitoids were reared from pupae of *Battus philenor* (Linnaeus); one of the specimens is *Theronia atalantae* (Poda), and the other six are *Apechthis annulicornis* (Cresson). The host pupae were all collected on October 3, 1960, at a single site ("North Carolina: above Crabtree to Betsey's Gap; 3956'; Haywood Co.; coll. Gertsch, Ivie"), and the wasps emerged in November 1960. The pupal remains were kept with the wasps, permitting confirmation of the hosts' identity.

These associations are particularly interesting because *Battus philenor* is considered relatively immune to attack by parasitoids. It may be protected by toxins acquired from its food plants, which are the various North American species of *Aristolochia* (Aristolochiaceae). The adults have long been recognized as the unpalatable models for a Batesian mimicry ring (Brower 1958); like many other species in the tribe Troidini (Nishida 1995), *B. philenor* sequesters substantial quantities of aristolochic acids to the adult stage (Sime, in prep.). Experimental evidence indicates that these compounds are unusually toxic, at least to non-adapted lepidopteran larvae (e.g. Miller and Feeny 1989). Haase (1893) was the first to link Aristolochiaceae-feeding with low parasitism rates, observing that *B. philenor* pupae never

yielded parasitoids while the pupae of the palatable mimics *Papilio troilus* Linnaeus and *P. glaucus* Linnaeus frequently produced ichneumonids.

Immature *B. philenor* are commonly collected and studied, and the considerable rearing data available in collections and in both published and unpublished studies suggest that larval and larval-pupal parasitoids are nearly nonexistent and pupal parasitoids rather rare. Among reports in the literature involving larvae, there is just a single record, lacking ecological data, for the tachinid *Compsilura concinnata* (Meigen) (Schaffner and Griswold 1934), which when in butterflies is a larval-pupal parasitoid (Ford and Shaw 1991). I have reared some 90 *B. philenor* (found as larvae) from the Blue Ridge Mountains of Virginia (a habitat similar to that for the new records), but obtained only butterflies. Rausher (1981), in an exhaustive study of *B. philenor* ecology in Texas, noted that in four field seasons no parasitoids emerged from several hundred field-collected larvae reared to adulthood. Other authors have collected pupae: West and Hazel (1982) reported no parasitoids in a Virginia study, though Sims and Shapiro (1983) found that *Brachymeria ovata* (Say) (Chalcididae) occasionally inflicts high mortality in some California populations of *B. philenor*. *Gambrus amoenus* (Gravenhorst) (= *nuncius* (Say)) (Ichneumonidae) has reportedly been reared from *B. philenor*, but the genus is thought only to attack

cocooned hosts, and Townes and Townes (1962) and Gupta (1983) consider this species a specialist on *Callosamia* and a few other Saturniidae.

Theronia atalantae is common and widespread; it is a polyphagous parasitoid of pupae apparently capable of both primary and secondary parasitism, though almost invariably found to be a secondary parasitoid when possible to investigate (Townes 1940). Almost always associated with Lepidoptera, it has been reared from at least 16 families, most frequently Lymantriidae and Lasiocampidae. (The apparent bias towards these two families may be an artifact of the attention that pests such as gypsy moth and forest tent caterpillars have received.) Whether the new record represents primary or secondary parasitism (perhaps on *A. annulicornis*) is not known. As a secondary parasitoid, however, its presence in *B. philenor* would not necessarily be remarkable: if the primary parasitoid detoxifies plant poisons in the lepidopteran pupa, it might itself become a non-toxic host for *T. atalantae*.

Apechthis annulicornis is a pupal parasitoid of Lepidoptera; it is reared less often than is *T. atalantae*, but a number of reports indicate that it has a broad host range, attacking *Neophasia menapia* (Felder & Felder) (Pieridae) and various species of *Choristoneura* (Tortricidae) and *Orgyia* (Lymantriidae) (Carlson 1979 and refs. therein). This record, together with those of *B. ovata* and *C. concinnata* (each of which attacks many families and over 100 species of Lepidoptera (Arnaud 1978; Halstead 1988)), indicates that *B. philenor* is the occasional host of several relatively polyphagous parasitoids that are reared much more often from other, less toxic Lepidoptera. This phenomenon may reflect a broad constitutive tolerance of plant allelochemicals on the part of the generalists: that larval and larval-pupal hymenopteran parasitoids are, in contrast, entirely lacking suggests that the unusual toxicity of aristolochic acids has prevented the

evolution of specialist, koinobiont parasitoids of *B. philenor*.

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Format and Preparation. Three copies of each manuscript, including copies of illustrations, should be submitted on letter size or A4 paper, double spaced, with at least 25 mm margins on all sides. On the upper left of the title page give name, address and telephone and fax numbers of the author to whom all correspondence is to be sent.

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Following acceptance of the manuscript, the author should provide the editor with one copy of the manuscript accompanied by a copy on diskette using DD, double sided computer diskettes—IBM compatible MS DOS 5.25 inch or IBM and Macintosh 3.5 inch diskettes. (Authors who do not have access to a computer should submit three copies of the manuscript.) The paper may be submitted in most PC and Mac word processor programs such as Microsoft Word, FullWrite Professional, WordPerfect, WriteNow, Nisus, MacWrite, or MacWrite II. If possible, all words that must be italicized should be done so, not underscored. Tables may be formatted in a spread sheet program such as MS Works or MS Excel. Text should be double-spaced typing, with 25 mm left and right margins. Tables should be put in a separate file. Diskettes should be accompanied by the name of the software program used (e.g., WordPerfect, Microsoft Word). Authors should keep backup copies of all material sent to the Editor. The Society cannot be responsible for diskettes or text mislaid or destroyed in transit or during editing.

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The Re-definition of Pimpline Genus *Hymenoepimecis* (Hymenoptera: Ichneumonidae) with a Description of a Plesiomorphic New Costa Rican Species

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Abstract.—An aberrant new species of the Neotropical genus *Hymenoepimecis*, *H. argyraphaga* Gauld n. sp. is described from Costa Rica, and the genus is redefined to accommodate this new taxon. A key is provided to identify the Costa Rican species. It is hypothesised that *H. argyraphaga* occupies a basal position in the genus, and is the sister group to all other species. The systematic position of *Hymenoepimecis* within the *Polysphincta* genus-group is discussed and a sister-group relationship with *Acrotaphus*, another New World genus, is demonstrated. It is suggested that this clade has arisen from within a paraphyletic “*Polysphincta*” complex, a cosmopolitan group that has yet to be resolved as a series of monophyletic taxa. Host records for the clade are summarised, and it is shown that the group are specialist parasitoids of orb-web spiders of the families Araneidae and Tetragnathidae.

Hymenoepimecis is an exclusively neotropical genus of ichneumonid wasps that belongs to the *Polysphincta* complex of genera, the “*Polysphinctini*” *sensu* Townes (1969), a monophyletic clade that has arisen from within the pimpline tribe Ephialtini (Wahl and Gauld, 1998). This clade is biologically unique within the Ichneumonidae because all members are koinobiont ectoparasitoids of spiders (Fitton *et al.* 1988; Gauld 1991; Gauld *et al.* 1998). Elsewhere in the Hymenoptera such an association is only known in a few Pompilidae (Wasbauer 1995). The female ichneumonid temporarily paralyses a spider by stinging it, and then attaches an egg either to the cephalothorax (the *Schizopyga/Dreisbachia* subgroup) or to the abdomen (the *Polysphincta* and *Zatypota* subgroups). The ichneumonid larva develops as an ectophagous parasitoid on the active spider. The *Hymenoepimecis* of southern Mesoa-merica are reasonably well-known (Gauld 1991; Gauld *et al.* 1998), but recently, a new species of has been found in Costa Rica which possesses certain plesiomorphic features that necessitate redefining the

genus. The purpose of this paper is to do this, and to describe and characterise this new species, in order to provide a taxonomic background for the following paper (Eberhard, 2000) which describes the biology of these fascinating insects.

Genus *Hymenoepimecis* Viereck

Epimecis Brullé 1846: 112. Type-species: *Epimecis bicolor* Brullé, designated by Ashmead 1900: 54. [Junior homonym of *Epimecis* Hübner.]
Hymenoepimecis Viereck 1912: 149. [Replacement name for *Epimecis* Brullé.]

Diagnosis.—Medium to large insects (fore wing length 6–14 mm) which are generally orange with black marking, with the wings from more or less hyaline to completely black, occasionally black and yellow patterned. Head somewhat globose, though abruptly declivous posteriorly; clypeus simple, not transversely divided, flat, apically truncate or slightly concave; mandible slender, strongly tapered with upper tooth distinctly the longer; palp formula 5:4; occipital carina very strong, dorsally convex, flange-like, continuous to base of mandible, with part just

below level of foramen magnum expanded to approach its counterpart below neck in some species; eyes large; antennae long and slender. Pronotum in profile from moderately to exceptionally long, with anterior margin reflexed, projecting below the occipital flange, with part immediately behind this modified into a anteriorly opening "pocket-like" structure; epomia entirely absent. Mesoscutum smooth and polished, more or less glabrous; notauli weakly to moderately impressed; mesopleuron polished, with epicnemial carina from completely absent to present ventrally, but laterally not reaching above level of lower corner of pronotum; metapleuron polished, with submetapleural carina usually absent, sometimes present anteriorly; propodeum quite short and evenly rounded posteriorly, without discernible carina, except for vestiges peripherally, but never with any enclosed area; propodeal spiracle more or less circular. Legs slender, but with fore legs variously developed, sometimes of similar size to middle legs, but often enlarged and with the fore femur conspicuously larger than middle femur; claws of female with large basal lobe, which in many species is high and short, but in one large South American species group is long and low, almost tooth-like; claws of male simple, with a small internal membranous vesicle. Fore wing with *3rs-m* entirely absent, but always with *2rs-m* quite long; hind wing with first abscissa of *M+Cu1* straight or weakly angled proximal to its centre; distal abscissa of *Cu1* present, joining *cu-a* from slightly to conspicuously closer to *M* than to *1A*. Metasoma slender, depressed, polished and more or less impunctate; tergite II with weak to strong oblique impressions anterolaterally, tergites III-IV with weak lateromedian convexities; ovipositor with a distally angulate basal swelling ventrally, with shaft from more or less straight to slightly up-curved, 1.0–1.4 times the length of the hind tibia,

weakly swollen centrally, apically elongately tapered to a fine sharp point.

Remarks.—*Hymenoepimecis* is a Central and South American genus, comprising eight described species (Yu and Horstmann 1997). Approximately ten undescribed species are known mainly from lowland or mid-altitude South America, occurring between sea-level and 1800 metres (in collections of American Entomological Institute, Gainesville, and The Natural History Museum, London). The geographical range of the genus extends from tropical Mexico and Cuba south to subtropical Southern Brazil (c. 29°S). In earlier systematic works (e.g., Townes 1969), the genus has been described as lacking both the epicnemial and submetapleural carinae, but recently an exception has been found in Costa Rica. This somewhat aberrant species has a discernible epicnemial carina and a more or less fully developed submetapleural carina. However, its generic placement is attested by the possession of two autapomorphies of *Hymenoepimecis*. First, the pronotum is mediodorsally modified to have a unique anteriorly opening "pocket-like" flange just behind the reflexed anterior margin. Second, the fore legs are enlarged, with the femora slightly larger than the middle femur. These apomorphies are unique within the Pimplinae, and strongly suggest that the slightly expanded *Hymenoepimecis* is a monophyletic group.

Systematic position.—*Hymenoepimecis* belongs to the *Polysphincta* genus-group (= *Polysphinctini sensu* Townes 1969), a clearly definable monophyletic clade of Ephialtini (Wahl and Gauld 1998). It is putatively the sister group of another primarily Neotropical genus, *Acrotaphus*, a relationship that is supported by three autapomorphies. First, the occipital carina is strongly raised, flange-like, and projects posteriorly to surround the anterior reflexed end of the pronotum. Second, the head is rounded (more or less "door-knob shaped") with the genae strongly nar-

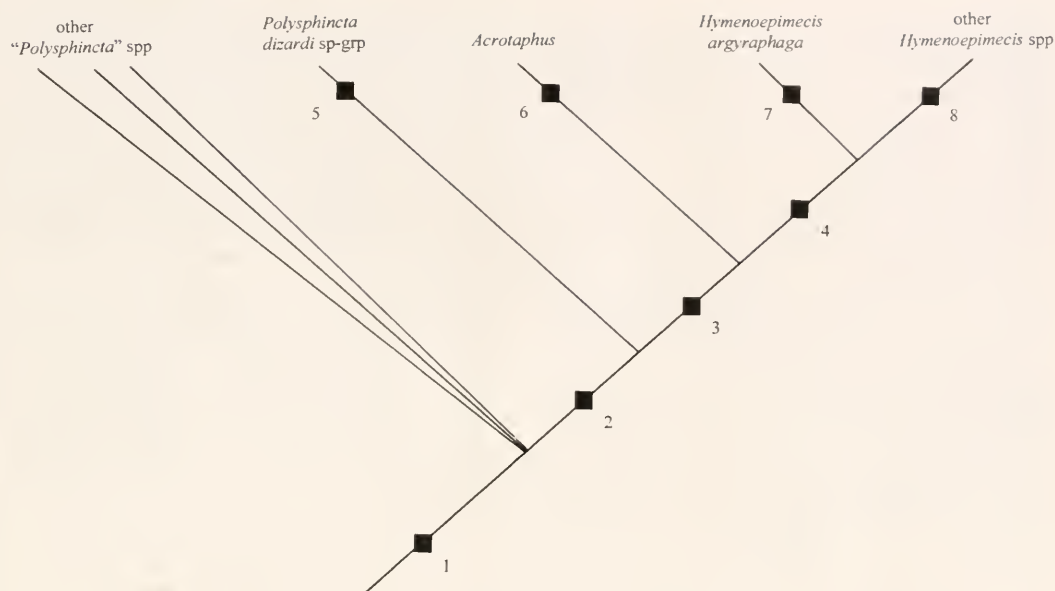


Fig. 1. Cladogram summarizing hypotheses of relationship of *Hymenoepimecis argyraphaga*. The derived features supporting these clades are: (1) long straight ovipositor with an angulate basal swelling; metasomal tergites II-III biconvex; (2) absence of epomia; enlarged ocelli and eyes; (3) occipital carina is strongly raised, flange-like, projecting backwards to surround the anterior reflexed end of the pronotum; head rounded with genae strongly narrowed from eyes to occipital flange; pronotum unusually elongate, with a long horizontal part mediodorsally; (4) pronotum mediodorsally with a forwardly directed "pocket-like" flange; fore legs enlarged, with the femora of similar size to or larger than the mid femur; (5) presence of a horizontal pronotal "shelf"; (6) cocoon without a caudal orifice; (7) wings uniformly blackish; (8) loss of epicnemial carina; loss of submetapleural carina. All characters are polarized with reference to the condition in *Tromatobia*.

rowed from the eyes to the occipital flange. Third, the pronotum is unusually elongate, with a long horizontal part mediodorsally.

The *Hymenoepimecis*/*Acrotaphus* clade is, in its turn, the sister group of yet another Neotropical group, the *Polysphincta dizardi* species-group (Gauld 1991). All three of these taxa lack any trace of an epomia, and are slender, highly polished insects with enlarged eyes and ocelli.

This entire lineage is part of the *Polysphincta* subgroup, a large cosmopolitan group of species that is characterized by having a uniquely basally swollen, ovipositor, and possessing biconvex metasomal tergites II-IV. The detailed phylogeny of this clade has yet to be fully resolved, but the genus *Polysphincta* (*sensu* Townes, 1969 and all subsequent authors) is apparently a paraphyletic assemblage, although

most of the species-groups within it are demonstrably monophyletic (Gauld 1991; Gauld *et al.* 1998) (Fig. 1).

All recorded hosts of the *Polysphincta* subgroup (i.e., "*Polysphincta*" s.l., *Acrotaphus* and *Hymenoepimecis*) are orb-web spiders of the families Araneidae and Tetragnathidae (Nielsen 1923; Townes and Townes, 1960; Fitton *et al.* 1988; Fincke *et al.* 1990; Gauld 1991). All records of "*Polysphincta*" are from Araneidae (e.g. Townes and Townes 1960; Fitton *et al.* 1988; unpublished records in Natural History Museum, London), whereas various species of *Acrotaphus* and *Hymenoepimecis* have been reared either from Araneidae or Tetragnathidae (Shannon 1913; Gauld *et al.* 1998; Eberhard 2000).

Costa Rican species.—Despite a very intensive country-wide sampling programme (Hanson and Gauld, 1995), spe-

cies of *Hymenoepimecis* are rather seldom collected in Costa Rica. Three species have been recorded (Gauld *et al.* 1998), but recently a fourth, undescribed species has been found on the Pacific coastal plain. Unusually for parasitoids, the majority of the Costa Rican *Hymenoepimecis* specimens in collections (25 out of 36) have been reared, rather than field-collected. Hosts are known for all of the four Costa Rican species. *Hymenoepimecis tedfordi* Gauld has not uncommonly been reared by W.G. Eberhard as a parasitoid of *Leucauge mariana* (Keyserling) (Tetragnathidae) (Gauld 1991), several specimens of *H. robertsae* Gauld have been found in Panama para-

sitizing *Nephila clavipes* (L.) (Tetragnathidae) (Fincke *et al.* 1990) and a single individual of the apparently rare *H. heidyae* Gauld has also been reared by W.G. Eberhard at La Selva, from *Cyrtophora nympha* (Simon) (Araneidae). The new species has been reared from by W.G. Eberhard from *Plesiometa argyra* (Walckenaer) (Tetragnathidae).

As mentioned above, the new species differs strikingly from all previously described *Hymenoepimecis* in possessing a number of plesiomorphic features. It is described below, after a key which will facilitate its separation from other, sympatric species.

KEY TO SPECIES OF HYMENOEPIMECIS PRESENT IN COSTA RICA

1. Fore wing uniformly blackish; submetapleural carina discernible, reaching at least 0.5 times length of metapleuron (Fig. 2); epicnemial carina present ventrally, although not laterally extended far onto mesopleuron. *argyraphaga* Gauld, sp. n.
 - Fore wing more or less hyaline, at most slightly infumate distally; submetapleural carina more or less absent (Fig. 3), at most discernible as a small denticle on extreme anterior margin of metapleuron; epicnemial carina only discernible as weak swellings ventrally either side of mid-line 2
 2. Metasoma with tergites all entirely black; sternite I with a low, rounded swelling posteriorly; pronotum long, so that distance from tegula to head is about 0.6 times distance from tegula to hind margin of propodeum *tedfordi* Gauld
 - Metasoma with tergites predominantly orange; sternite 1 with a large acute or nasute protuberance near posterior margin (Fig. 3); pronotum exceptionally long, so that distance from tegula to head is greater than 0.7 times distance from tegula to hind margin of propodeum 3
 3. Hind coxa and femur orange; sternite I with an acute, thorn-like ventral projection; female with ovipositor 1.0–1.2 times as long as hind tibia; hind leg slender, with tibia and tarsus combined, more than 0.9 times fore wing length. *robertsae* Gauld
 - Hind coxa and femur extensively black; sternite I with a high laterally compressed nasute ventral protuberance; female with ovipositor 1.3–1.4 times as long as hind tibia; hind leg fairly stout, with tibia and tarsus combined about 0.6 times fore wing length. *heidyae* Gauld
-

Hymenoepimecis argyraphaga Gauld, sp. n.

Female.—lower face elongate 0.8 times as broad as high (from clypeofacial suture to base of antenna), flat, centrally smooth and impunctate, laterally with fine setiferous punctures bearing long fine hairs;

head in dorsal view with gena long, strongly but evenly narrowed behind eyes; ocelli of moderate size, the lateral one separated from eye by about 0.7 times its own maximum diameter; lower end of occipital carina only very weakly raised, not produced mesally to approach its counterpart on the midline. Pronotum

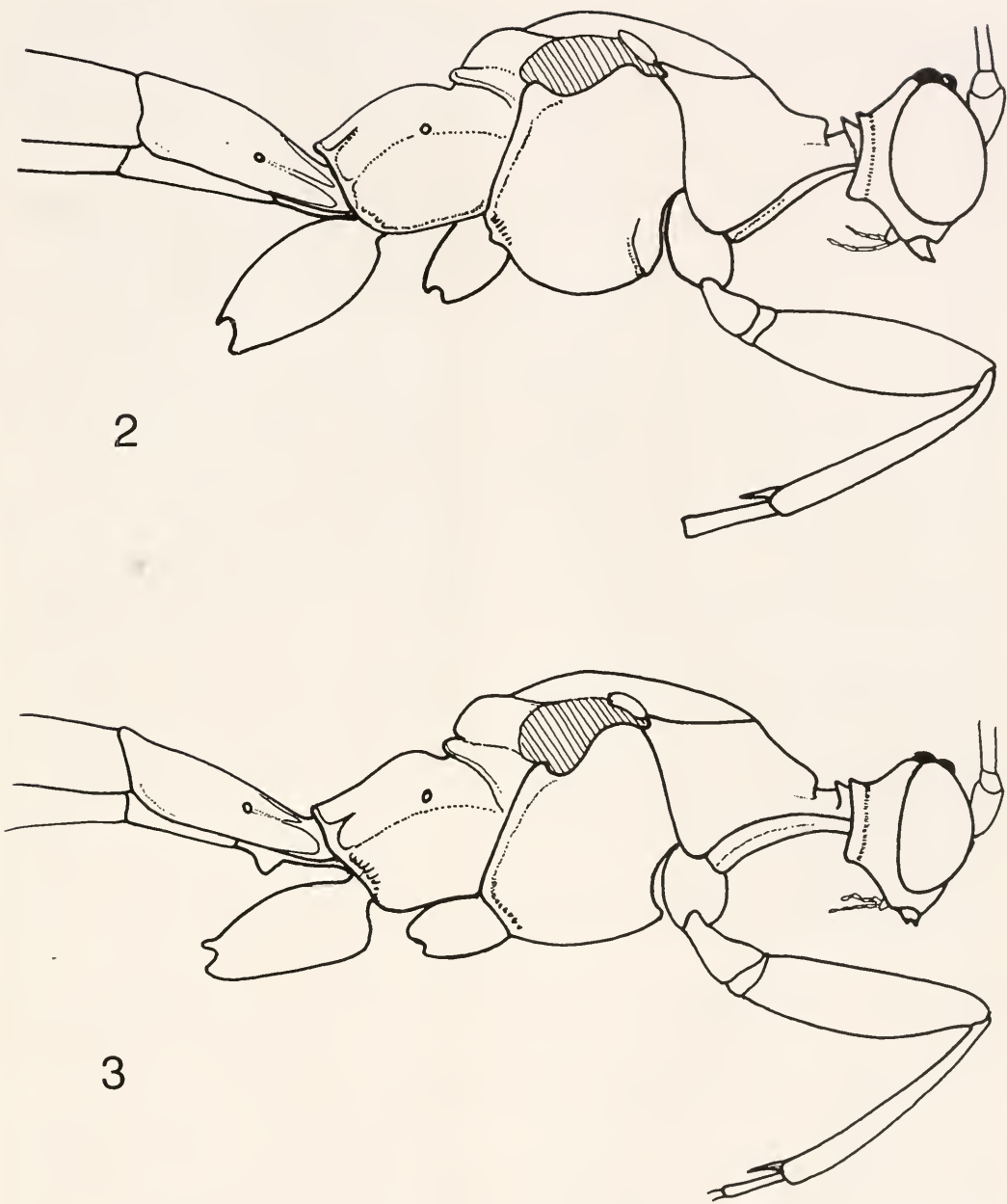


Fig. 2–3. 2, *Hymenopimecis* spp. 2, *H. argyraphaga*, head, and mesosoma, lateral. Note the comparatively plesiomorphic body shape, in comparison with Fig. 3. 3, *H. robertsae*, head, and mesosoma, lateral, showing typical body form of members of this genus.

long so that distance from tegula to head is about 0.6 times the distance from tegula to hind margin of pronotum; scutellum in profile strongly convex; mesopleuron smooth and polished; epicnemial carina

present ventrally, weak but extending across the ventral portion of the mesosoma so that it is just visible in profile; metapleuron quite convex, smooth and polished, glabrous; submetapleural carina ex-

tending at least 0.5 of length of pleuron, usually more or less complete; propodeum smooth, laterally with very fine setiferous punctures. Fore wing length 8.0–8.5 mm; *cu-a* slightly distal to base of *Rs&M*; *2rs-m* about 0.6 times as long as abscissa of *M* between *2rs-m* and *2m-cu*; hind wing with abscissa of *Cu1* between *M* and *cu-a* 0.3–0.4 times as long as *cu-a*. Hind leg moderately long and slender with tibia plus tarsus 0.6 times the fore wing length; hind tarsal claws short, with a deep basal lobe (this condition is common to all Costa Rican species, but in South America a large number have the claw unusually long, and the lobe low, sometimes tooth-like). Metasoma moderately slender, tergite I 1.4–1.5 times as long as posteriorly broad, centrally evenly convex, with lateral carinae present only anteriorly bordering the anterior concavity; sternite I with a low rounded medioventral prominence; tergite II 1.1–1.2 times as long as posteriorly broad, with weak oblique grooves anterolaterally; tergite III about 1.2 times as long as posteriorly broad with a median anterior swelling, centrally glabrous and with scattered hairs around the periphery of the tergite; tergites IV–V similar in sculpture and pilosity; ovipositor 1.0–1.1 times as long as hind tibia.

Head black with mouthparts yellowish brown; antenna blackish; mesosoma orange-brown; metasoma with anterior two or three tergites orange anteriorly and broadly infuscate posteriorly, the area of infuscation increasing in extent and intensity on each tergite progressively towards the hind end, which has the tergites black; ovipositor sheath black. Anterior two pairs of legs orange-brown, the hind legs blackish, with bases of coxae brownish. Wings blackish infumate, pterostigma and veins black.

Male.—similar to female in structure and colour; claspers black.

Material examined.—Holotype ♀, Costa Rica, Puntarenas Province, Parrita, 20 m,

i.1996 (Eberhard) (Natural History Museum, London). Paratypes: 3 ♀, 3 ♂, same locality as holotype (Eberhard) (American Entomological Institute, Natural History Museum, London and INBio, Santo Domingo, Costa Rica).

Remarks.—*Hymenoepimecis argyraphaga* may easily be recognized in Costa Rica by its black wings. I have seen no other species, described or undescribed with uniformly black wings, although several South American species, including *H. heteropus* (Kriechbaumer) have black and yellow patterned wings. *Hymenoepimecis argyraphaga* is also the only species I have seen in the genus with discernible epicnemial and submetapleural carinae, and unlike other species it does not have the lower end of the occipital carina produced mesally more or less to meet its counterpart medioventrally and partially close the oral fossa. The possession of these plesiomorphic features strongly suggests *H. argyraphaga* is one of the more basal species in the genus. This is supported by other features. *H. argyraphaga* has short, deep hind tarsal claws, like *Acrotaphus*, whereas most South American species have highly modified long, low claws with a tooth-like basal lobe. Additionally sternite I of this species is not modified but it generally has a thorn-like protuberance in other species. Furthermore, although enlarged, the fore legs of *H. argyraphaga* are not as massive as many of the apparently more derived species in the genus.

These preliminary suggestions about both the phylogenetic position of *H. argyraphaga* within *Hymenoepimecis* and of this genus with respect to others in the genus-group, have important implications for understanding the evolution of biological traits within this uniquely adapted group of ichneumonids.

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I thank Bill Eberhard for allowing me to study his reared specimens. David X. Wahl and I are collaborating closely in an attempt to unravel the phyloge-

netic interrelationships of the Pimplinae, and the discussion above has benefited from his insight. I thank David Wahl and Andy Bennett for their comments on the manuscript.

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The Natural History and Behavior of *Hymenoepimecis argyraphaga* (Hymenoptera: Ichneumonidae) a Parasitoid of *Plesiometa argyra* (Araneae: Tetragnathidae)

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Abstract.—Larvae of the koinobiont ectoparasitoid *Hymenoepimecis argyraphaga* Gauld used a series of different adaptations as they matured to hold onto the abdomen of their host spider, *Plesiometa argyra*, its web, and the larval cocoon: the first instar did not leave the egg chorion, which was glued to the spider by the female wasp when she oviposited; the second instar used two pairs of ventral abdominal protuberances to help hold onto both the first larva's molted cuticle and to what was probably a sheet of coagulated spider hemolymph that adhered to the larva and to wounds that it made on the spider's abdomen; the early final instar grasped the shed second instar cuticle that remained attached to the coagulated hemolymph with the ventral surface of its abdomen; and the late final instar used a row of mobile dorsal protuberances with sharply curved spines that grasped lines of a unique web that the larva induced the spider to spin just before killing it, and then the larva's own cocoon silk. The pupa used a pair of toothed protuberances at the tip of the abdomen to stay at the upper end of its cocoon. Other aspects of the wasp's biology that are described include infanticide by adult females; aculeate-like lack of use of the ovipositor to oviposit; manipulation of host web-spinning behavior, apparently by means of a fast-acting larval secretion with long-term effects; manipulation of host bleeding; alternative tactics in attacks on spiders; use of pheromones by females to attract males; cocoon spinning behavior; and a bias to parasitize female rather than male spiders.

Although Ichneumonidae is undoubtedly one of the largest of all animal families, remarkably little is known about the behavior of the larvae. Excluding studies of foraging behavior, adult behavior is also poorly studied (e.g., Hanson and Gauld 1995). The neotropical polysphinctine pimplines are no exception. The more derived polysphinctines are known to be koinobiont ectoparasitoids of spiders (Gauld 1995, Wahl and Gauld 1998), and several European species were observed in careful detail by G. C. Bignell (1898) and E. Nielsen (1923, 1928, 1929, 1935). There is apparently only a single study of a neotropical species, that of Fincke et al. (1990) on *Hymenoepimecis robertsae* Gauld (for probable identification see Gauld et al. 1998). The general natural history of this

species resembles that of some European polysphinctines. It is an external koinobiont on a spider, the tetragnathid *Nephila clavipes* (L.). The female temporarily paralyzes the host by stinging it in the cephalothorax, and then glues an egg on its abdomen. Spiders with a wasp egg or a young larva are active, and build apparently normal prey capture webs and feed while the larva feeds by sucking the spider's hemolymph and gradually matures. The spider's webs become more irregular and reduced one to two days before the larva kills it and constructs its pupal cocoon, which is attached to the spider's web. A second species, *H. tedfordi* Gauld, parasitizes another tetragnathid spider, *Leucauge marinae* Keyserling (Gauld et al. 1998), but nothing more is known about

Table 1. Degree of development of eggs in the ovaries (6–7 ovarioles/ovary) of female wasps of different ages (N = number of wasps; W = white eggs apparently ready to be laid, Y = yellow, still-immature eggs; uric acid determined on arbitrary scale of 0–3).

Age of wasp outside cocoon (hrs)	Mean length and color of eggs (mm)				Amount of uric acid	N
	Largest (basal) egg in each ovariole	Color	Second largest egg	Color		
6–12	0.15 ± .18	Y	0		2, 3	2
24	0.22 ± .20	Y	0		1, 2, 2	3
approx. 36	0.82 ± .04	W	0.27 ± .02	Y	0	1
approx. 60	0.59 ± .27	W/Y	0.08 ± .17	Y	1, 1	2
approx. 72	0.84 ± .02	W	0.68 ± .21	Y	0, 1	2
approx. 84	0.84 ± .05	W	0.56 ± .14	Y	0, 0	2

its behavior. The present observations concern a third, newly discovered species, *H. argyraphaga* Gauld (Gauld 2000).

MATERIALS AND METHODS

Field observations were made in January and February of 1999 and 2000 in the undergrowth of plantations of approximately 10–15 m tall African oil palms (*Elaeis guianensis*) near Parrita, Puntarenas Province, Costa Rica (elevation about 20 m). Spiders were checked for parasites in the field with a 10× hand lens while holding the spider by its legs, and some wasp attacks were observed using a 2× headband magnifier. Spiders and immature stages of the wasps were transported to San Antonio de Escazu (1300 m), and reared there. All observations were at room temperature, and durations of some immature stages of the wasps may be slight overestimates, due to the lower temperatures in San Antonio. Dissections and measurements were made using recently killed individuals in saline solution. Bleeding and coagulation were studied by poking a minuten pin through the abdominal cuticle of mature female spiders.

Video recordings of behavior were made using a Sony CCD-TR700 camcorder with +7 closeup lenses. Voucher specimens of wasps have been deposited in the The Natural History Museum, London, the Museo de Insectos of the Universidad de Costa Rica, and the U. S. National Museum of Natural History. Spe-

cies names follow Fitton et al. 1988, and Gauld et al. 1998. The species observed by Bignell (1898) is cited as an undetermined polysphinctine because of confusion regarding its identity (M. Shaw, pers. comm.).

RESULTS

Adults

Maturation of eggs.—Dissections of females kept with access to water and honey after they emerged as adults showed that females emerged without any well-developed eggs, but with massive fat bodies that contained large amounts of small white pellets (presumably uric acid) (Table 1). Over the next 3–4 days the fat and uric acid diminished, and the yellow developing eggs gradually grew and changed to large, whitish eggs that were apparently ready to lay. Eggs matured one by one, rather than synchronously, both within a given ovariole and in different ovarioles.

Sexual behavior.—Males were seen repeatedly in the field. They flew slowly, and did not stay in any given area. They repeatedly hovered near the tips of leaves at the tops of undergrowth plants. Their flight patterns were inappropriate to encounter pupal cocoons, which were generally lower and deeper in the vegetation. Males showed no signs of sustained aggression when they encountered each other, although one male flew into and

knocked another from his perch on a leaf tip.

Two interactions between males and females were observed in the field. Both involved virgin females that had recently emerged from their cocoons. Each female rested on the side of her cocoon for at least 90 min, where she eliminated small white masses (presumably uric acid) and periodically cleaned herself. No males approached the females as they rested on their cocoons. Eventually each female flew 1–2 m and landed on the tip of a leaf about 1.5 m above the ground, near the top of the undergrowth. Close inspection of one of the females using the headband magnifier as she rested on the plant failed to reveal any obvious sign of pheromone emission (extension of abdomen, drops of liquid, eversion of membranous sac). Nevertheless, one female had only been on the leaf for about 65 s when a male arrived. The wind was too slow and erratic to determine whether or not he arrived from downwind. He landed directly on the female, and immediately curled his abdomen forward ventrally and copulated. After 5–10 s, the female began to walk, the male gave a couple of brief buzzes of his wings, the pair separated, and both wasps flew away.

The second virgin female moved from one leaf tip to another twice before being approached by a male. This male flew persistently from tip to tip of the pinnules of a palm leaf that was just downwind of the female, landing briefly on each. Then he flew about 1 m upwind and returned to search again. On his third or fourth approach the male encountered the plant on which the female was resting, and landed near her. She immediately took flight, and the male continued to investigate leaf tips in the vicinity for about 1 min more before moving on.

Hunting for spiders.—I witnessed 14 attacks (eight successful) in their entirety, and parts of five others. The early stages of all attacks were similar. The wasp hov-

ered about 10–30 cm from the spider, facing toward it as it rested at the hub of its more or less horizontal orb for several seconds. Usually the attack was launched from about 10–15 cm above the spider. The wasp darted rapidly at the spider and grasped it through the web with her legs. The wasp did not consistently strike from downwind of the spider, and in one case she first hovered at one side of the spider, then flew over it, turned 180° to face it again, and attacked from the other side. Thus at least the final stage of host localization appeared to depend on visual rather than chemical cues. Wasps were more likely to attack larger spiders (see section below on parasitism rates).

There was always a brief struggle during which it was not possible to resolve exactly what was happening; probably the wasp jabbed rapidly and forcefully with her ovipositor while she grasped the spider with her legs. When I was finally able to resolve the animals' positions (usually after 10 s or less), the wasp's ovipositor was inserted into the anterior end of the spider's cephalothorax; in four cases it was apparently thrust into the spider's mouth, in two it was just to the side of one chelicera, and in another it was on the anterior side of the spider's first coxa. This first long sting lasted for up to 120 s, during which the spider's struggles gradually became less vigorous. In two attacks on relatively small spiders the sting was only about 10–20 s. After withdrawing her ovipositor, the wasp performed a series of apparent jabs with her ovipositor, and in two cases she inserted it again into the spider's cephalothorax. By this time the spider rested completely immobile at the hub of its web (Fig. 1). Paralysis generally lasted for approximately 5–10 min.

The wasp then positioned herself under the spider's abdomen, facing posteriorly (Fig. 1), and bent her abdomen ventrally and repeatedly wiped, jabbed and rubbed with the distal portion of her ovipositor for as long as several minutes over the an-

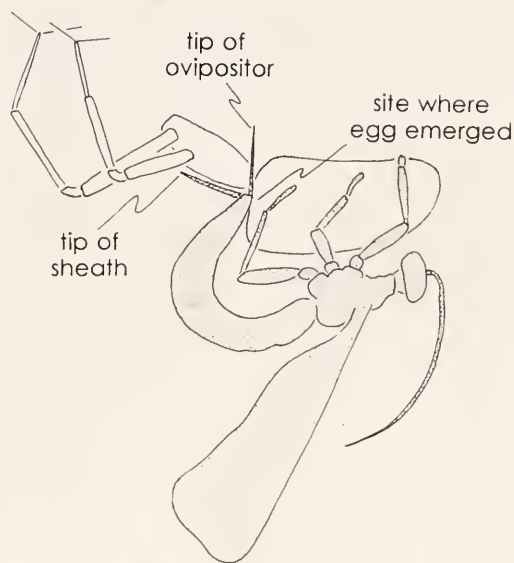


Fig. 1. Diagrammatic illustration of a female wasp hanging on paralyzed spider at the hub of its web and ovipositing at the point indicated (drawn from field notes; it is not certain whether the wasp's tarsi held the spider, as in the drawing, or the web just above it).

terior and dorsal surface of the spider's abdomen. These probing movements probably served to locate, perhaps to sting, and to dislodge the eggs or larvae of previous wasps that had attacked this spider. In one case, repeated probing movements of the ovipositor in the vicinity of a first instar or early second instar larva may have included one or more insertions of the ovipositor into the larva, and they finally resulted in the larva being levered off of the spider's abdomen and onto the middle portion of the wasp's ovipositor. The wasp then knocked off the larva to the ground with cleaning movements, and soon afterward laid an egg of her own. In two other cases an egg (identity confirmed by subsequent collection) was moved onto the middle of the ovipositor and then fell to the ground.

Of 16 parasitized spiders collected in 1999 with eggs or first instar larvae on their abdomens, four gave further evidence that larvae are sometimes removed:

there were one or more groups of larval feeding scars on portions of the abdomen that were inaccessible to the current larva in two cases, and there were larval feeding scars but no larvae and only an egg in two others. In contrast, only one spider was doubly parasitized, carrying both an egg and a second instar larva. Similar data from 2000 gave even more dramatic evidence of infanticide. Of 55 mature female spiders, nearly half (26) had at least one patch of feeding and bleeding scars on her abdomen (the total of additional patches was 43; the maximum on one spider was four). Only three spiders were doubly parasitized. It should be noted that these data undoubtedly underestimate the frequency of infanticide, because removal of eggs from hosts cannot be detected using feeding scars.

Finally the wasp oviposited. Holding her ovipositor sheaths elevated dorsally and her ovipositor pressed against the anterior surface of the spider's abdomen (Fig. 1), she pressed the tip of her abdomen near the surface of the spider's abdomen briefly. The egg emerged from the tip of her abdomen (and *not* from the tip of her ovipositor), and adhered to the spider's abdomen. Within about 30 sec after ovipositing the wasp flew away. In no case did a wasp give any sign of attempting to feed on the spider. Although eggs were generally placed on the anterior dorsal surface of the spider's abdomen, the exact sites varied widely (Fig. 3). The oval egg was glued tightly on its ventral side to the spider's abdominal cuticle. Two eggs which were observed being laid and then inspected periodically hatched between 48 and 72 hours later.

An incomplete observation of one interaction indicated that the wasps have an alternative hunting strategy that depends on deceiving the spider. When they were first encountered, the spider was resting at the edge of its orb, and the wasp was hanging immobile from radii in the free zone near the hub, facing downward with

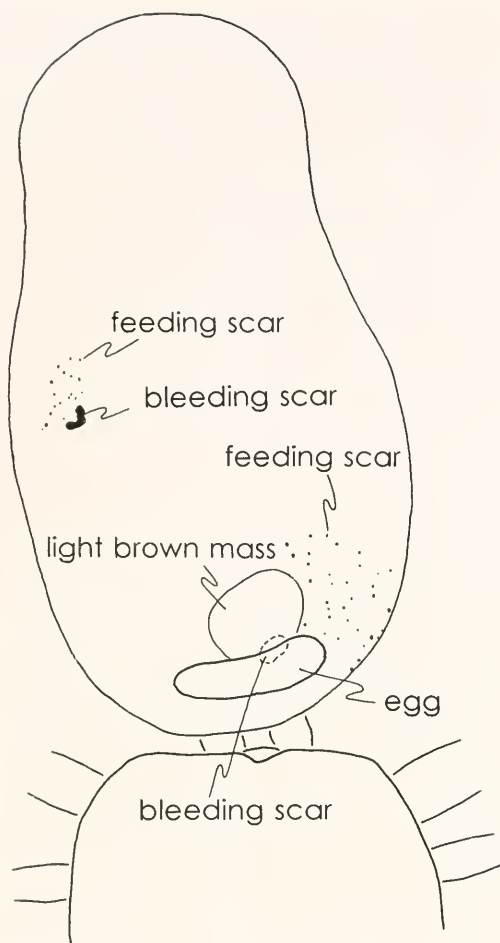


Fig. 2. Evidence of two infanticides. The anterior surface of the abdomen of a *P. argyra* spider bears a wasp egg, and two arrays of feeding and bleeding scars (dark spots) that were presumably produced by wasp larvae that had hatched from eggs laid previously, but that were then removed when subsequent female wasps attacked this spider.

most or all of her legs extended stiffly. The wasp appeared to be either dead or paralyzed, and a gentle nudge of the wasp with my finger confirmed that she was completely immobile. She remained motionless until the spider returned to the hub about 5 min later. As the spider arrived at the hub, however, there was a sudden tangle of legs and it quickly became clear that the wasp's ovipositor was inserted near the spider's mouth. Soon the

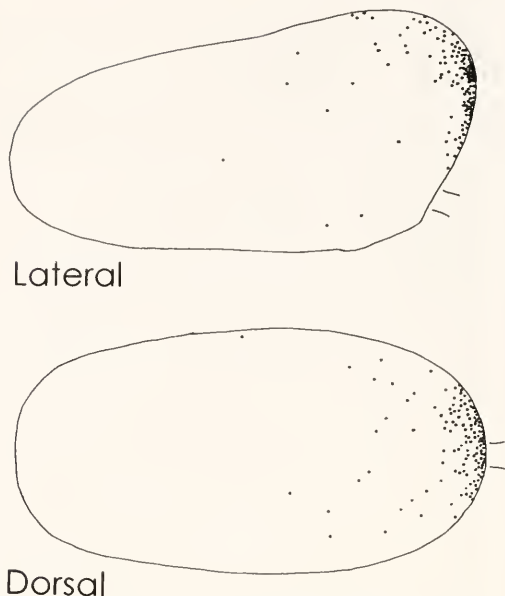


Fig. 3. Schematic representation of 125 sites of the anterior ends of egg and the bleeding scars of the larva on the spider's abdomen in lateral and dorsal views.

spider became immobile, and the wasp, which had fooled both the spider and me by playing dead, proceeded to oviposit.

Wasps also showed a certain flexibility in oviposition behavior. When one spider began to move after the wasp had spent several minutes attempting to remove an egg, the wasp moved to its anterior end and apparently stung it again, then resumed egg removal.

Failed wasp attacks illustrate possible kinds of selection on spiders to avoid attacks. In one case the spider's orb was inclined so that much of its surface was between the wasp and the spider as the wasp hovered above and to the side of the spider; when the wasp finally struck, it hit and was arrested by the orb before reaching the spider, the spider moved away, and the wasp flew on. In two other cases (one first seen after the interaction had already begun), the spider hung from its dragline about 10–15 cm below the hub, and when the wasp struck from above it hit and was arrested by the orb, and thus

did not reach the spider. The wasp then hovered nearby, and the spider twice climbed very rapidly to the hub but immediately dropped again. Finally the spider dashed to the edge of the web, and the wasp flew on. The presence of web threads between the spider and the wasp that were not right next to the spider thus appeared to reduce the likelihood that a wasp's attack would succeed. A final failure occurred when a gentle wind apparently made it more difficult for the wasp to hover steadily near the spider, and she eventually crashed into the web and then flew away. Windier sites may thus be safer for spiders.

Larvae

First instar.—The first instar larva apparently burst open one end of the egg, but only its anterior end emerged from the chorion. Its posterior end remained lodged inside the chorion, and thus attached to the spider. The first instar larvae possessed neither the ventral nor the dorsal structures used by later instars to hold onto the spider and its web. A small brown spot or feeding scar (see below) appeared on the spider's abdomen just beyond the edge of the chorion of recently emerged larvae. The subsequent gradual accumulation of feeding scars on the spider's abdomen, which were always restricted to the vicinity of the larva's head, indicated that the larva fed at small holes it made in the spider's abdomen (Figs. 2, 4). As the larva grew, it gradually protruded more and more from the egg chorion. The head, the entire thorax, and the first two to three abdominal segments were free by the time the larva was ready to molt to the second instar, and by then there were 8–10 feeding scars on the spider's abdomen. The first instar lasted between 58 and 69 hours ($N = 2$).

First instar larvae were able to remain attached when the spider molted, as evidenced by two pale, soft newly-molted adult spiders each having a first instar lar-

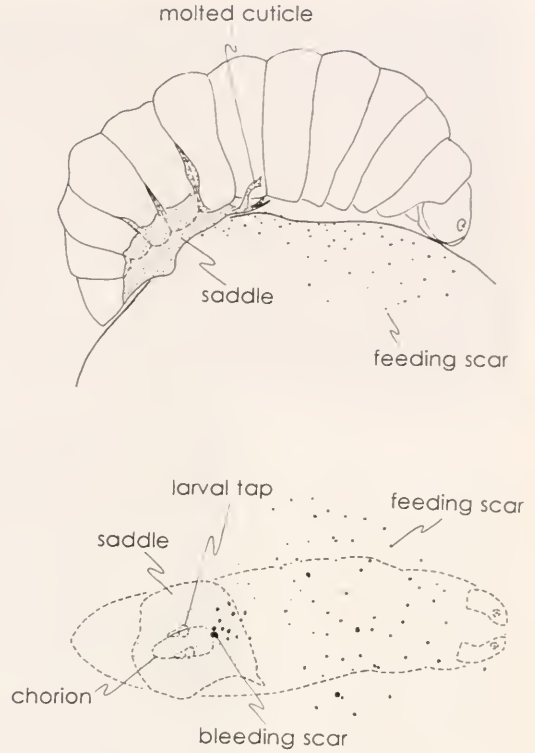


Fig. 4. Pattern of brown scars on the abdomen of a spider carrying a second instar larva in lateral view (above) and ventral view, looking outward through the spider's cuticle (below). The sites of insertion of the larva's taps were not visible, and were determined by subsequent dissection.

va attached to its abdomen. In both cases (and in two other spiders) a portion of the cuticle of the previous instar (usually the dorsal portion of the cephalothorax plus a wrinkled portion of the abdomen) was attached to the spider's abdomen, apparently at a bleeding scar (Fig. 4).

Second instar.—The transformation from first to second instar was not witnessed, and the probable series of events was reconstructed from preserved specimens. The newly molted second instar larva was completely outside the collapsed egg chorion. The larva's ventral surface rested on the flattened, shed first instar larval cuticle, and this cuticle in turn rested on a large, stiff sheet of brown amorphous material (Figs. 4, 5) (the "saddle" of Nielsen

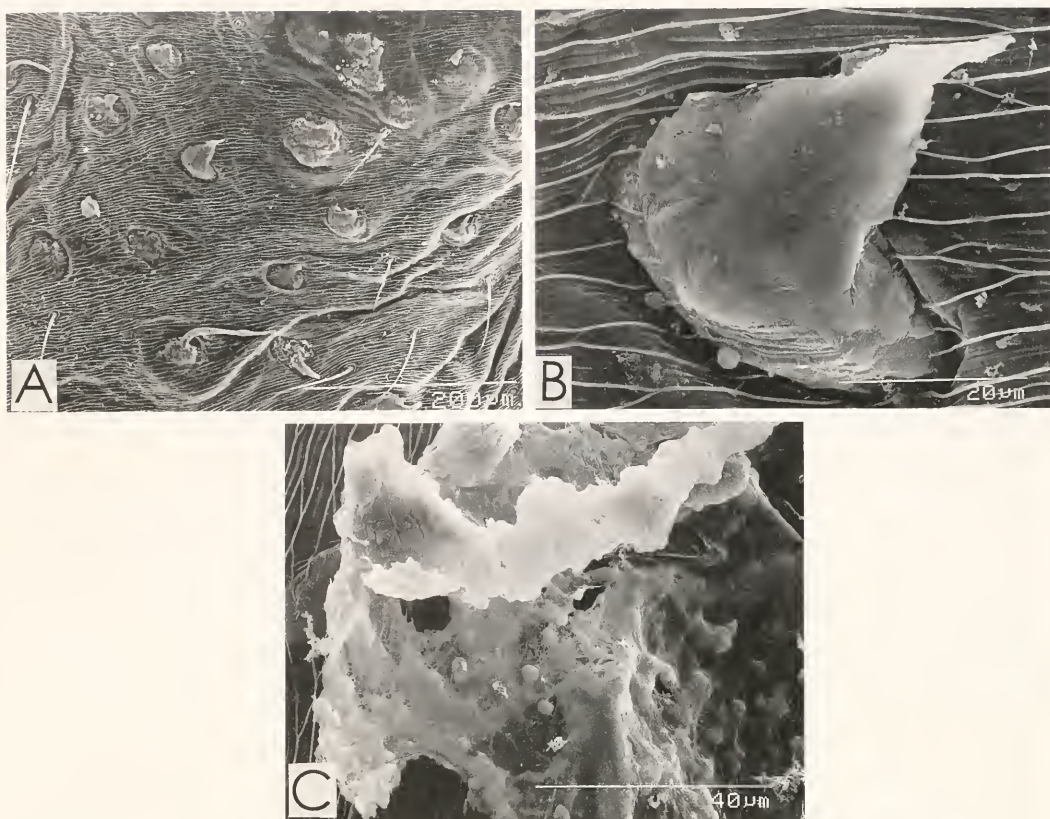


Fig. 5. Micrographs of apparent feeding scars (A and B) and saddle material (C) of a second instar larva on the corrugated abdominal cuticle of a spider. Many feeding scars were produced into more or less conical protuberances of different shapes (A). A closeup view (B) shows that the scar material (presumably coagulated hemolymph) flowed over the corrugated abdominal cuticle around the perforation before hardening. The "saddle" material is amorphous, and is not a shed larval skin.

1923). The empty egg chorion was on the inner surface of the saddle that contacted the surface of the spider's abdomen. The saddle was probably composed of coagulated hemolymph, and had a different form in each parasitized spider. It was tightly attached to the spider's abdomen near the open end of the egg. The anterior end of the shed larval cuticle was near the anterior edge of this sheet, indicating that molting probably involved a split of the first instar's cuticle along the dorsal midline of most of the larva's body, rather than a rearward sloughing of cuticle as occurred at pupation (see below).

The saddle adhered to both the ventral surface of the larva on its outer side, and

to the spider's abdominal cuticle on its inner side, and could be peeled away intact from both except at the central attachment area. Here it was attached tightly to the spider's abdomen at several brown spots that were similar to the feeding scars mentioned above but larger (Fig. 4). In some cases projections of the saddle extended into the larva's intersegmental grooves (Fig. 4), indicating that the saddle had been a liquid at some time after the larva molted. Two pairs of protuberances ("taps" of Nielsen 1923) on the ventral surface of the larva's segments 8 and 9 were inserted deeply into the saddle (and perhaps also the shed skin) (Fig. 4). They adhered so tightly to the saddle that it was

difficult to separate the larva from it without damaging the taps.

The second instar larva apparently continued feeding as before, as brown feeding scars gradually accumulated on the side of the spider's abdomen on which the larva's head rested. Many feeding scars were produced externally into more or less conical shapes whose tips pointed anteriorly on the abdomen (toward the larva's head) (Fig. 5). The spider's pattern of coloration, which was due to soft tissues under the transparent abdominal cuticle, was often (though not always) intact in areas with feeding scars. Thus larvae probably usually consumed hemolymph, rather than digesting other internal tissues.

When the spider's abdominal tissue was dissected away, there were no inward extensions of either the feeding scars or the attachment spots; all were relatively smooth on their inner surfaces. Smaller feeding scars were concentrated nearer the egg (where the larva presumably fed when it was smaller—Fig. 4). The feeding scars had a remarkably regular distribution, with larger spaces between larger scars (Figs 2, 4).

Saddle-like puddles of hemolymph did not form at experimental wounds (approximately 0.1 mm diameter) made by puncturing the abdominal cuticle with a fine pin, despite the fact that these holes were larger than feeding scars (about 40 μm in dia—see Fig. 5). In nearly all cases the hole was immediately sealed by a small plug when the pin was withdrawn. This plug, which was little more than the diameter of the hole, was initially liquid when touched with the pin, but hardened to a solid within 10–15 s, and darkened to a light brown color. In two cases in which a small sheet (up to about 0.3 mm in diameter) of hemolymph emerged from the wound before a plug formed, the sheet did not turn dark brown, but instead acquired a nearly transparent golden color. The inner surfaces of these wounds, revealed by dissecting away underlying tis-

sue after the specimen was preserved in alcohol, were smooth and dark, similar to those of feeding scars.

The number of second instar larvae prior to their final day (below) in collections made in 2000 was approximately equal to the number of eggs and of first instar larvae (62 second instars, 73 eggs, 57 first instars). Assuming that the egg stage lasts about 2.5 days and that the relative numbers of the different immature stages were fairly constant over the space of a few weeks (supported by the similarity in numbers in the surveys made on 28–30 Jan. and 9–10 Feb, 2000— $\chi^2 = 2.7$, $\text{df} = 3$, $p > 0.4$), this suggests that the second instar normally lasts two to three days in nature. It can also last much longer, however. The second instar lasted 46 days in one case in which the spider was kept captive with only infrequent feeding. Spiders carrying first and second instar larvae occurred on apparently normal orbs in the field (Eberhard in prep.).

The true number of larval instars is not certain. Fitton et al. (1988) speculated that all pimelines may have five larval instars, on the grounds that *Pimpla* does, with "the middle three being very similar and hard to distinguish". If so, then the stages designated here as first and second may actually represent three or four stages that I was unable to distinguish. The distribution of the widths of the head capsules of 81 larvae (Fig. 6) did not clarify this. There were two peaks within the range of sizes classified here as first instars, while several final instar larvae (which can be recognized unequivocally by the dorsal tubercles covered with curved spines) were substantially smaller than several others which were clearly in the previous instar (the curved spines were visible, but were covered with a transparent layer of cuticle). It may be that head capsule width is not constant within an instar, as some sclerites may be connected by elastic membranes.

Final ("third") instar.—There were sev-

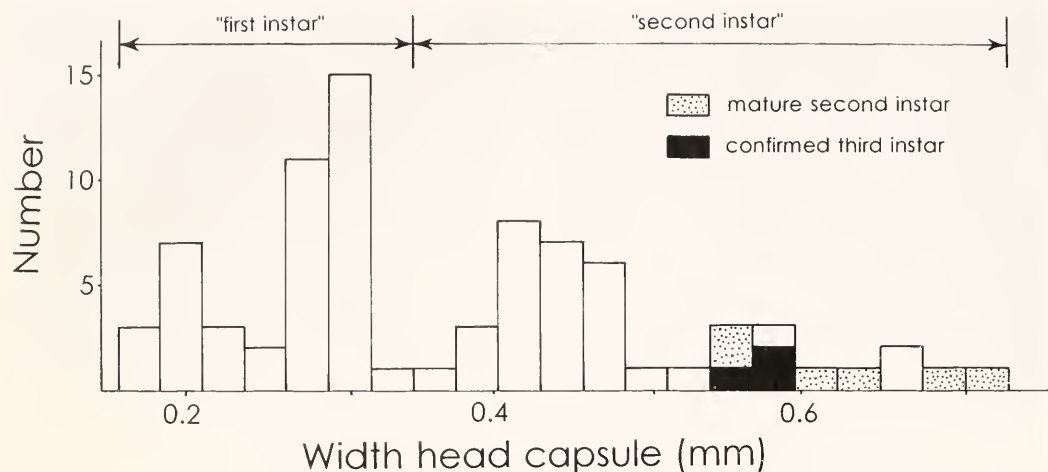


Fig. 6. Distribution of head capsule widths of 81 larvae, and approximate limits of classifications of larval instars used in this study. "Confirmed" final (supposed third) instar larvae had hooked spines on dorsal tubercles; "mature" second instar larvae had hooks that were clearly visible under the larva's dorsal cuticle.

eral differences between second and third (final) instar larvae. The dorsal surfaces of eight segments (3–10 posterior to the head) of the final instar, which had been smooth in previous instars, each had a retractable two-lobed tubercle whose tips were covered with curved spines (Fig. 7). There was a pair of taps on the ventral surface of segments 8 and 9 as in the second instar, but they were free (Fig. 8), and not embedded in the saddle. The shed cuticle of the second instar formed a compact sheet bent into a cup. It adhered tightly to the saddle, apparently where the

taps of the cuticle of the second instar were inserted. The saddle, in turn, still adhered tightly to the spider's abdomen. The larva grasped the posterior edge of the sheet of second instar cuticle between its final (13th) segment and the bulging ventral margin of its penultimate (12th) segment (Fig. 8C). In addition, the larva's head capsule was substantially different (Fig. 9).

The final instar was relatively brief. All larvae raised to final instars or collected in the field as swollen second instars or as final instars killed the spider the following

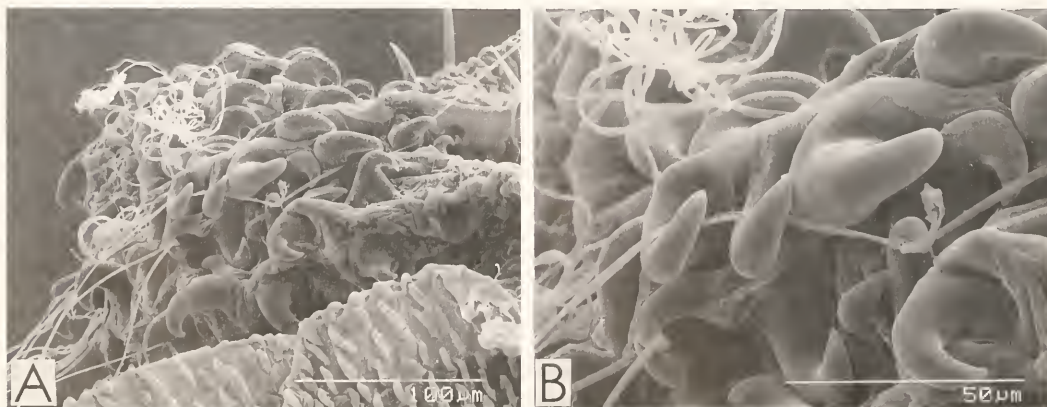


Fig. 7. Hooks on a dorsal tubercle of a final instar larva that have snagged tangled spider silk.

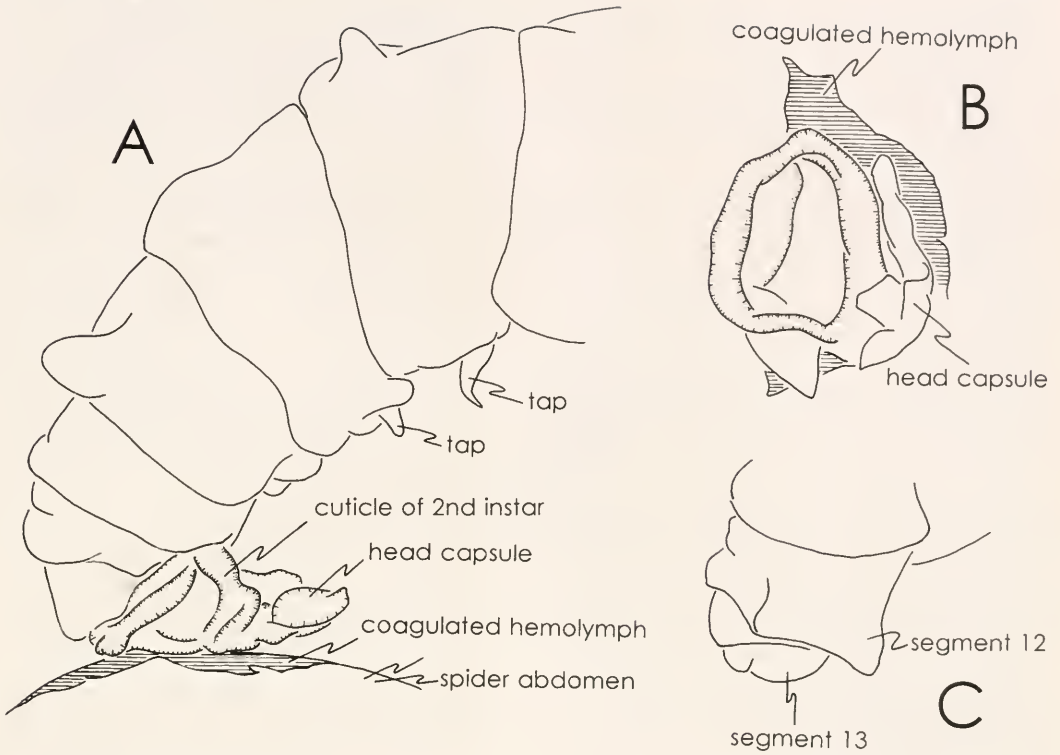


Fig. 8. (A) Attachment of the final instar larva to the spider's abdomen, seen in lateral view. (B) Dorsal view of the cup-shaped mass of larval cuticle. (C) Lateral view of the posterior tip of a larva removed from its attachment to the spider, showing the protruding ventral surface of segment 12 that gripped the edge of the cup of larval cuticle.

night. An estimate from field collections of swollen last day second instar larvae and early final instars on spiders in 2000 was in accord with the estimate of a duration

of only one day or slightly less (only 18 individuals, as compared with 73 eggs and 57 first instars).

The final day in the spider's life was eventful. At least some spiders built an orb of apparently normally design and size in the morning, but during the day the second instar larva grew to an estimated one quarter to one third of the volume of the spider's abdomen. At about 23:00–01:00 the spider built a modified "cocoon web" of a few highly reinforced radial lines that was especially appropriate to support the cocoon the larva would build the next evening. In two cases the larva repeatedly extended its body nearly straight while the spider built the cocoon web.

The cocoon web and the behavior employed to build it are described elsewhere



Fig. 9. Antero-lateral view of head capsule of final instar larva.

(Eberhard in press, in prep.). Briefly, the spider used one portion of one subroutine of frame line construction over and over to build a small number (mean 3.8 ± 1.4 , $N = 39$) of radial lines, each of which is a cable composed of many individual lines. This web did not resemble any prey capture, resting, molting, or egg sacs webs normally built by *P. argyra*. Experimental removal of larvae showed there to be a complex, long-term effect on the spider's behavior that is probably mediated chemically. Typical cocoon web construction followed in three cases when a swollen second instar larva was removed from a spider that had been kept in a confined space until about midnight, when it would probably have begun cocoon web construction. These spiders were still alive the next day, and the next evening they each built a second typical cocoon web.

Thirteen other spiders from which the larvae were removed between 22:00 and 02:00 built structures that were neither normal orbs nor cocoon webs. Three of these spiders were observed building. They placed radial lines from the hub to the edge using the behavior used to construct typical cocoon webs (Eberhard in prep.), but also broke and reeled up these lines while moving back toward the hub. The final products were sparse networks of more or less radial lines in which there were large accumulations of reeled up silk (fluff) near the hub. All of these spiders were also alive and active the next morning.

Soon after it finished the cocoon web, the parasitized spider became immobile. All of nine spiders were dead or completely immobile by 03:00 (in one checked under the microscope, the heart had stopped beating), and the larva had lifted the anterior portion of its body above that of the spider to grasp the lines of the web with its dorsal protuberances (see below). The posterior portion of its body remained attached to the saddle. The larva proceeded to suck the spider dry over the course of

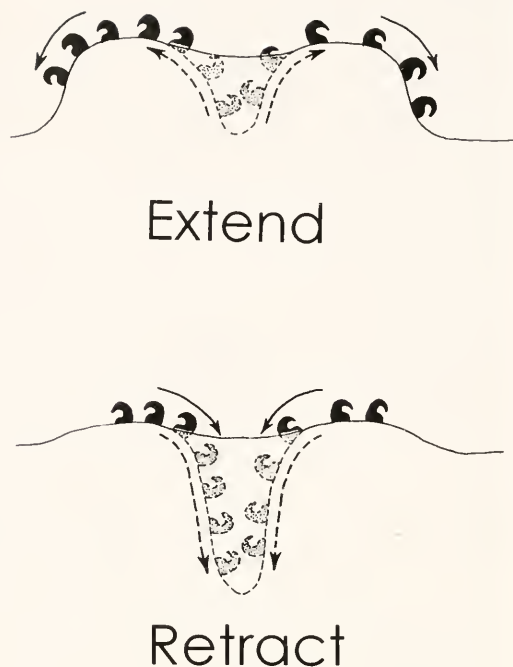


Fig. 10. Diagrammatic representation of the movements of the curved spines at the tip of a turret that caused lines to be snagged when the tubercle was everted (above), and release of lines when it was retracted (below).

the morning, feeding first on the spider's abdomen and then on its cephalothorax.

The mechanism by which the larva grasped and released lines with its hook-covered dorsal tubercles was revealed by observations under a dissecting microscope. The tubercles were extremely mobile, and could be extended so that the distance of their tips from the dorsal surface of the larva's body was up to about one third of the diameter of the body. They could also be retracted rapidly so that the entire tubercle and all of its hooks disappeared completely into a pocket on the dorsal surface of the larva's body. Because the spines near the tip of each tubercle were sharply curved, eversion of the tubercle resulted in a grasping effect, as lines were snagged by the curved spines (Figs. 7, 10). The spines released their holds on lines when the tubercle was retracted into the larva's body.

Coordination of tubercle movements was complex. When the larva moved its anterior end, the anterior-most three tubercles often contacted the web only sporadically. When the tubercles were out of contact they were often everted and retracted simultaneously. In contrast, the more posterior tubercles, which usually held onto threads and supported the larva's weight, moved less often and sequentially. When the larva moved its entire body forward or backward, each tubercle that was holding silk released its hold by retracting, everted toward the next tubercle where it seized silk, and the next tubercle then released its hold and was everted toward the next, and so on. These stepping movements swept along the larva's body rapidly, and it sometimes stepped with several tubercles in a second.

Feeding by a final instar larva on a dead spider was observed under a dissecting microscope. The first stage of a feeding bout involved apparent searching and hooking of the mouthparts against the surface of the abdominal cuticle. I was not able to discern any pattern to these movements, nor any responses to the brown feeding scars already present. Finally, sometimes after minutes of such searching, the larva's head came to rest at a particular site where it apparently began to produce a hole.

After a minute or so, the larva began to suck. The rhythmic movements of its head were reminiscent of those of a nursing human infant (Fig. 11). Approximately once every second the larva pulled its head slightly away from the abdomen without breaking contact with its mouthparts, then sprang slightly toward it again. In one case it was possible to see the flow of the spider's tissues through the transparent cuticle of the abdomen as the larva sucked. Clumps of abdominal tissue flowed steadily into the larva's mouth. Two timed feeding bouts lasted about 30 min. They ended when the larva pulled its head away and rested immobile for sev-

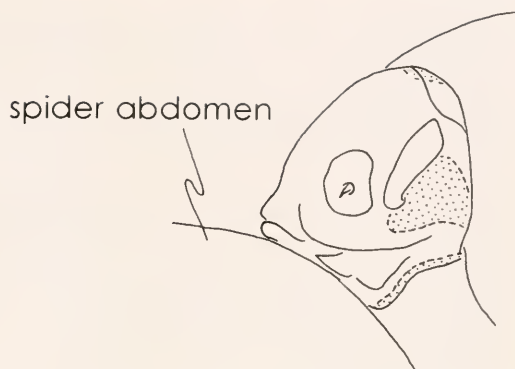


Fig. 11. Diagrammatic representation of the head of a feeding larva; the stippled areas pulsed as the larva sucked.

eral minutes. When the larva withdrew its head after feeding, there was a small amount of clear liquid on the surface of the spider which quickly dried up; no hole was visible, nor did a brown spot form.

On three occasions it was clear that the larva interrupted sucking and that a clear liquid flowed from its mouth into the spider for several seconds. This liquid formed a small pool around the point where the larva's head contacted the abdomen, and it also flowed under the cuticle, as deduced from brief movements of spider tissue away from the larva's mouthparts. Presumably the clear liquid contained digestive enzymes.

When feeding ended, the larva freed itself from the now more or less empty but intact cuticle of the spider, and it dropped to the ground below. This process was not observed directly, and it was not clear whether the larva actively unhooked the spider's tarsal claws from the web. The saddle was still attached to the discarded carcass of the spider, and bore the imprint of the larva's last two abdominal segments (Fig. 8). In two cases the discarded carcass of the spider represented about 50% of the larva's weight: larvae which weighed 15.7 and 26.2 mg discarded carcasses that weighed, respectively, 6.1 and 10.4 mg.

The now somewhat greenish larva hung motionless, curled ventrally as it held the

web with its dorsal tubercles, for the rest of the daylight hours. Larvae in the field were remarkably coordinated in killing and consuming their hosts. All but one of 13 final instar larvae found before 13:00 were still feeding on the dead host, while all of 11 found between 13:00 and 17:00 had dropped the spider and were resting immobile at the hub of the cocoon web.

Cocoon construction began soon after darkness fell (about 18:40). The process of first attaching the cocoon's suspension line to the spider's web, then extending the line below the web, and then forming the walls of the cocoon was accomplished as the larva slowly inched backward over a period of up to an hour or more. The larva maintained a hold on silk lines with its dorsal tubercles at all times. At first it held onto the silk of the spider's cocoon web, then later onto the suspension line of its cocoon.

The larva produced a silk line (or lines?) from its head by pulling away from a point where the line was attached, and then attached this line to others by tapping or rubbing its head against them. The first lines were attached repeatedly to the lines at the hub of the spider's web, and were often somewhat dispersed. Gradually they condensed into a single multi-stranded line as the larva moved backward a few millimeters. The suspension line of the cocoon was produced by a simple sequence of movements repeated over and over (Fig. 12A). First the larva attached its line to the spider's web, and drew out a line by moving its head downward. Usually it paused immobile for several seconds, and then moved its head farther, toward the posterior end of its body, which was bent anteriorly. The head usually dabbed or scraped repeatedly against the posterior portion of the body, gradually touching points more and more toward its dorsal surface. During the last few scrapes it often dragged its mouthparts across its rearmost dorsal tubercle. Probably these movements often resulted

in snagging the line on the tubercle. The larva then extended the rear portion of its body downward, thus probably pulling more silk, and it moved its head back up to contact the spider web above and make another attachment there. The usual duration of one complete cycle was about 5–10 s.

By repeating this sequence of spinning movements over and over, the larva gradually produced a bundle of lines that ran from the attachments to the spider web down to the rear end of its own body and back up to the web again. This bundle would form the suspension line of the cocoon. The suspension line was lengthened when the larva grasped the bundle with the dorsal tubercles, moving rearward along the bundle, and then resuming spinning movements. Eventually the upper attachments of spinning movements were to the suspension line itself rather than to the spider's web.

The final stage of cocoon construction also involved a simple pattern repeated over and over (Fig. 12B). The larva moved its head to touch the edge of the bundle of lines already spun near its lower end, then pulled away a short distance and then moved back to touch the edge again slightly farther up, and repeated this behavior until it reached the suspension line, then bent downward again to begin the next series of attachments near the bottom edge of the bundle. The larva thus gradually extended the bundle laterally to form a bag-like sheet that enclosed the posterior portion of its body. Later the bag was gradually extended upward to enclose the upper portion of its body also. The bag was closed by addition of lines to its inner surface, about 4–5 hrs after cocoon construction began. Once the bag was closed it was more difficult to observe the larva's behavior, but it was clear that it sometimes turned 180° to face downward and add more lines to the bottom of the cocoon. Cocoon construction contin-

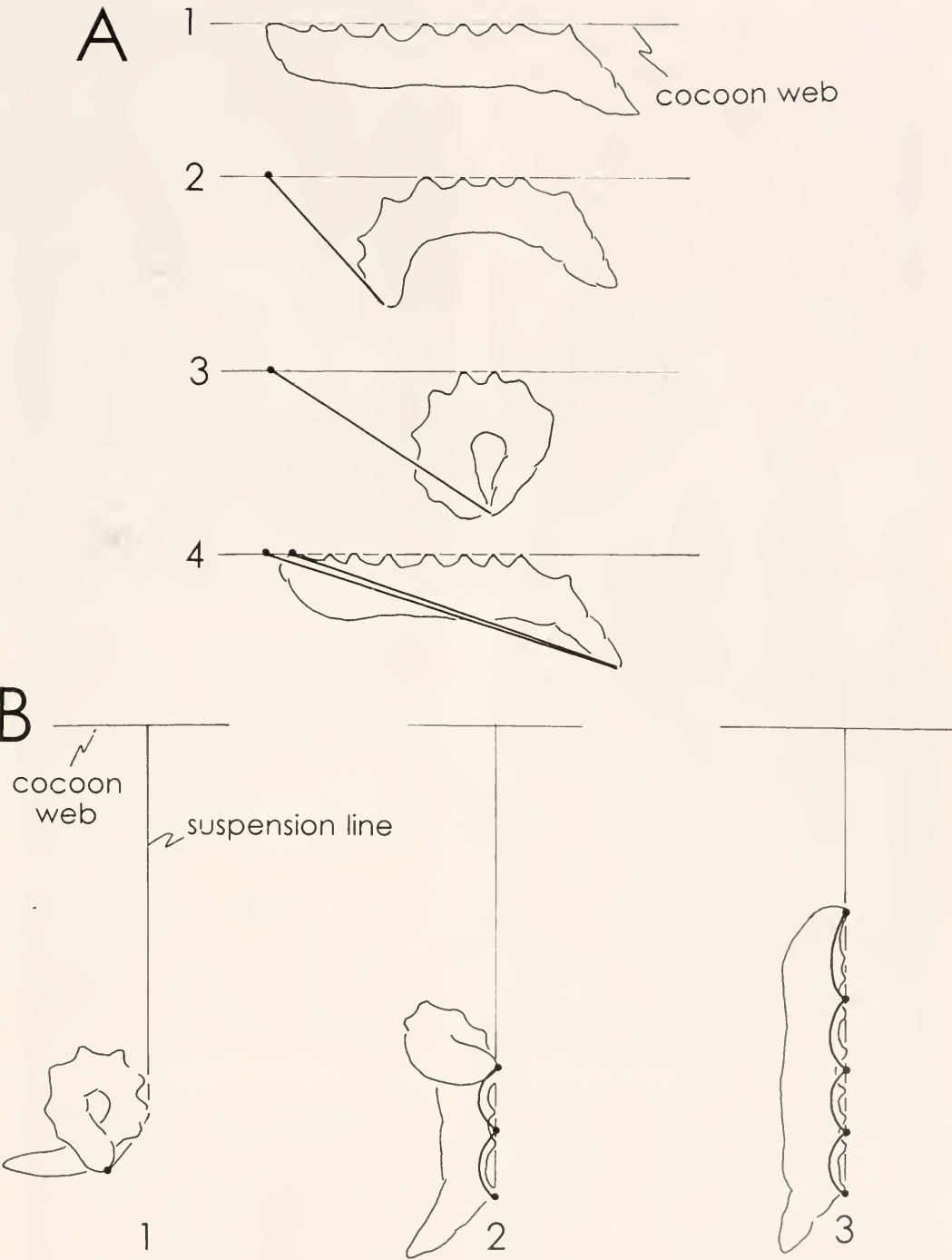


Fig. 12. The sequence of movements as a larva built the suspension line of the cocoon (A) and when it began the cocoon itself (B).

ued through the night and the following morning.

Cocoons spun in captivity were all very light yellow in color, and gradually darkened over the next day or so. Those kept in closed containers out of the light were especially pale. Some of those found in nature were dark yellow, while most were bright orange. About 36–65 hrs. after cocoon construction began, the larva ejected its meconium, which generally fell through the circular hole at the bottom of the cocoon (Gauld et al. 1998). One larva molted to a pupa between 4 and 5 days after killing its host.

Pupa

Pupal behavior could not be observed directly, except for the short series of rapid dorso-ventral contractions of the abdomen usually made when the pupa was disturbed. Indirect evidence suggests that the pair of toothed prominences near the tip of the pupal abdomen, which were immobile, served to engage the tip of the abdomen against the inner wall of the cocoon, and thus hold the pupa at the upper end of its cocoon. All of seven living pupae checked by cutting a slit in the side of the cocoon were wedged at the upper end of the cocoon (the pupa occupied only an estimated average $83 \pm 6\%$ of the length of the cocoon). All pupae observed in cocoons were oriented with the head upward, and the circular emergence slit made by the adult was always at the upper end of the cocoon. Presumably this position served to keep the pupa's posterior end away from the meconium or the shed larval skin that was sometimes present at the bottom tip of the cocoon. Four adults emerged 10–12 days after cocoon construction, so the pupal stage lasted about a week. A total of 26 males and 38 females were raised from field-collected cocoons (not significantly different from 50:50 with χ^2 Test).

Other aspects of natural history

Rates of parasitism.—Mature female spiders were approximately ten times more heavily parasitized than were mature males (42.9% of 203 females compared with 6.9% of 72 males in 1999; 66.4% of 125 females vs. 3.2% of 62 males in 2000). The rate of parasitism of mature females earlier in 1999 (27–30 Jan) was lower than that later (2–5 Feb.) the same year (26.5% of 83 females compared with 50% of 120 females— $p < 0.001$ with χ^2). In contrast, the first survey in 2000 showed a higher rate for mature females than for the second survey that year (84.2% of 57 females on 28–30 Jan., vs. 51.5% of 68 on 9–10 Feb., $p < 0.001$ with χ^2). The rates of parasitism of mature males did not differ significantly for the two surveys in either year (7.1% of 28 compared with 6.9% of 44 in 1999, 3.1% of 32 vs. 3.3% of 30 in 2000).

Mature females were also more heavily parasitized than were immatures. In the first survey of 2000, 84.2% of mature females, but only 50.8% of 63 penultimate females, 39.5% of 43 penultimate males, and 25.7% of ante-penultimate nymphs were paralyzed (all rates were lower than that for mature females, $p < 0.001$ with χ^2 ; ante-penultimates were less parasitized than penultimates, $p = 0.033$ with χ^2). Similarly, penultimate spiders showed less evidence of infanticide (25 cases in 73 spiders, compared with 43 cases among 55 mature females, $p < 0.001$ with χ^2).

Enemies of the wasp.—Mortality in the cocoon was relatively low. Seven *Conura* of two different species, one in the *immaculata* group of the subgenus *Ceratosmicra*, and the other in the *vau* group of the subgenus *Conura* (Chalcididae) were raised from 105 inhabited cocoons collected in the field in 1999, and 4 of 85 empty cocoons had *Conura* sp. pupal skins, giving a total rate of 5.8%. An eighth female *Conura* was captured after being first seen resting on the side of a cocoon in the field.

Two days later this cocoon contained a young pupa of *H. argyraphaga*, suggesting that the late larval or early pupal stage of the host was parasitized. Two chalcidids that pupated in captivity each had a dead *H. argyraphaga* pupa in the same cocoon, and three empty cocoons collected in the field that had a pupal cuticle of *Conura* also had the remains of a *H. argyraphaga* pupa.

Other field mortality of stages in cocoons, presumably due to predators, was noted as removal of the entire cocoon from the cocoon web (8 cases), or complete removal of the cocoon's contents (associated with a large hole in the side in two cases, and with multiple small ragged holes in two others). Two mature female spiders in the field carried dead first instar larvae, but the cause of death was not clear.

Two adult *H. argyraphaga*, one male and one female, were found dead at the hubs of orb webs of the araneid *Gasteracantha cancriformis* (L.), despite the fact that the wasps seem to be chemically defended. Even recently emerged adults less than four hours old released a pungent odor when grasped between the fingers (neither large second instar larvae nor their host spiders had any perceptible smell or taste). One tug of war between a larva and a salticid spider at the hub of a new cocoon web resulted in the larva's loss of the dead spider, and nearly resulted in predation on the larva.

One further predatory event may have been an artifact, but it illustrates another potential danger to the wasp. A penultimate instar male spider with a swollen second instar larva was placed in a plastic bag in a more or less cramped position. An hour or so later, the spider was feeding on the anterior end of the larva, which was still attached posteriorly to the saddle. In no other case did a parasitized spider exhibit any behavior directed toward the larva on its abdomen.

DISCUSSION

Chemical manipulation of the host.—Larvae of *H. argyraphaga* manipulate both the behavior and the physiology of their hosts. The changes in the spider's behavior which resulted in the production of the otherwise unique, strong "cocoon" web that is particularly well designed to sustain the wasp's cocoon, involved induction of the first steps of one subprogram of orb web construction that were repeated over and over to the exclusion of others (Eberhard in press, in prep.). Experimental removal of larvae showed that these behavioral changes occurred as a result of a fast-acting substance or substances with long-term effects introduced into the spider just before the larva molted to the final instar. It appears that the larva's induction of one type of building behavior and repression of others may represent separate effects, as their manifestation was partially uncoupled by early removal of the larva (Eberhard in prep.). Induction by the final instar during cocoon web construction seems unlikely, due to both the softness of the final instar's pale head capsule soon after molting, and the complete cocoon webs obtained after the mature second instar was removed. In contrast, the death of the spider soon after the cocoon web was finished probably resulted from material injected by the final instar larva just after the cocoon web was finished, when it began to feed; spiders did not die when the larva was removed just prior to this molt.

Manipulation of spider bleeding occurred when the larva molted from the first to second instar, and resulted in the production of the saddle. The form and the position of the saddle suggest that liquid hemolymph emerged in unusually large amounts from the large holes in the spider's abdomen and did not immediately coagulate as usual (one saddle was about 0.9×1.5 mm, while the largest puddle of hemolymph produced by wound-

ing with a minuten pin was only about 0.27 mm in diameter). These holes were probably made just before the first instar larva emerged from the egg chorion to molt, because the newly molted second instar larva would have had a soft head capsule, presumably incapable of biting through the spider's cuticle. Judging by the apparent difficulty that the larger final instar larva had in perforating the spider's relatively tough cuticle, it probably took the first instar larva many minutes to make these large holes. The spider's hemolymph must have coagulated only slowly, and was evidently still liquid after ecdysis occurred, since saddle material sometimes flowed part way up the side of the second instar larva's cuticle (Fig. 4). Liquid hemolymph may have helped the larva adhere to the spider during the delicate period after it had abandoned its egg but was still a first instar and thus lacked grasping structures. The extensive flow of hemolymph and the long delay before it coagulated contrast with the small plugs of rapidly coagulated hemolymph at puncture wounds made with a fine pin. Presumably the larva added something to the spider's blood which retarded coagulation.

One other possible manipulation was the inhibition of molting by host spiders. The evidence is only indirect, however. Despite the fact that wasp larvae were able to remain attached when their host molted (as also occurs in other polysphinctines—Nielsen 1923), and that the rate of parasitism of penultimate male spiders was not significantly different from that of penultimate females (39.5% of 45 penultimate males versus 50.8% of 63 penultimate females in 2000), the rate of parasitism of mature males was only about a tenth of that of mature females the same year. Of 32 parasitized penultimate and ante-penultimate spiders reared for two weeks, not a single spider molted. The only evidence that spiders molted after being parasitized involved wasp larvae that

were very small when they were found, apparently soon after the spider's molt. Perhaps these larvae had not been hatched long enough to inhibit the molt.

Comparisons with related wasps.—There are many points of similarity between the behavior and natural history of *H. argyraphaga* and *H. robertsae* (Fincke et al. 1990), and with polysphinctines of other genera (Bignell 1898, Nielsen 1923, Fitton et al. 1988, Gauld et al. 1998). Females of *H. robertsae* may also attack spiders at the hubs of their webs, sting the spider in the cephalothorax to produce a temporary paralysis (Fincke and colleagues witnessed only what were apparently aftermaths of attacks, however), and lay an egg on the anterior surface of the abdomen. The female wasp also moves the ovipositor back and forth over the spider's abdomen (for up to five min) prior to ovipositing, and thus may also remove previously deposited eggs or larvae. Fincke et al. (1990) found four doubly parasitized spiders, however. Thus *H. argyraphaga* is the only species yet found in which it is certain that females kill the offspring from previous attacks on the host. The selective advantage of infanticide seems obvious. Only one of probably several hundred cocoon webs seen in the field had two cocoons, and only one of these two produced a wasp. A second doubly parasitized spider was killed and consumed in captivity by the larger larva, while the smaller larva fell to the ground (still alive) with the discarded cadaver of the spider.

Similar use of the egg chorion to hold onto the spider occurs in *Acrodactyla madida* (Haliday) (= *Polysphincta clypeata*), though Nielsen's (1923) drawings indicate that the egg of this species is also used by larger larvae, rather than only the first instar as in *H. argyraphaga*. The dorsal tubercles ("warts") of the final instar are similar in form and placement to those of *Zatypota albicoxa* (Walker) (= *Polysphincta eximia*) and *Polysphincta tuberosa* Gravenhorst (Nielsen 1923). The two pairs of ven-

tral taps on segments 8 and 9 of the final instar larva of *H. argyraphaga* also resembled those of most of the species studied by Nielsen (1923), except that he recorded three pairs (on segments 7, 8 and 9) in *P. tuberosa*.

The use of the sharply hooked setae on the tubercles to seize silk lines was apparently identical in all other species observed. Although Fincke et al. (1990) made no direct observations of larval behavior of *H. robertsae*, their Fig. 3 clearly shows dorsal tubercles on a large larva, leading to the supposition that they also have curved spines and are used to hold onto the spider's web. Bignell (1898) seems to have been correct in stating that lines were released by retracting these tubercles rather than by extending them, as also occurs in a pimpline ichneumonid that is probably fairly closely related to Polysphinctini, *Tromatobia oculatoria* (Fabricius) (Nielsen 1923) (Nielsen 1923 may have been mistaken in describing the opposite process of releasing by extending in *Z. albicoxa*).

Only some details of how larvae of *H. argyraphaga* hold onto the host spider resemble descriptions of other species. Insertion of the paired ventral taps into a mass of material (the saddle) that adheres to the spider's abdomen, as described for second instar *H. argyraphaga*, has been seen in several other species (Nielsen 1923, 1935), though no difference was noted between second and final instar larvae. Nielsen (1923) stated that the cuticle of the first instar larva of *Z. albicoxa* was "glued to the host", but this was not true for *H. argyraphaga*. In conjunction with this idea, Nielsen supposed that the saddle consisted of larval exuviae (Nielsen 1923, 1935), and this has been reiterated by later authors (e.g., Fitton et al. 1987, 1988). It seems likely, however, that the portion of the second instar's saddle that adhered to the host was coagulated spider hemolymph as in *H. argyraphaga* (Figs. 4, 5), rather than first instar larval cuticle. In fact Nielsen (1923) mentioned that wounds

might be involved in allowing the larva to adhere to the spider.

None of the descriptions of other species mentioned the final instar larva's change to hold onto the shed cuticle of the second instar with its terminal segments instead of its taps, as seen in *H. argyraphaga*. The mature larva's ability to release the spider in all of the species in order to pupate (presumably by relaxing the muscles that squeezed the shed cuticle), and the especially active movements of the posterior tip of the larva during the only molting process that has ever been observed directly (Nielsen 1923: 148–149 on *Z. albicoxa*; "... the repeated attempts at fixing made by the hind end ..."), suggest that similar changes may occur in other species.

Both Nielsen and Bignell also noted that the larva of respectively *Zatypota* and an undetermined polysphinctine utilized the posterior part of the abdomen to pull out silk lines during cocoon construction, although their descriptions differ in details. It is not clear whether these differences were due to differences between species or, as supposed by Nielsen (1923), to differences in the precision of observations. The cocoons of *H. robertsae* were similar in form and color to those of *H. argyraphaga*. Increases in the duration of the larval stage when the host is feeding poorly, as in *H. argyraphaga*, probably also occurs in other species (Nielsen 1923).

Females of *H. robertsae* were also larger than males, as is common among pimplines (Gauld et al. 1998), implying that ovipositing females fertilize or refrain from fertilizing the egg on the basis of the size of the prey. If molting by the host is inhibited by *H. argyraphaga*, then the size of the spider when it is attacked will correlate with the size of the resulting wasp. Both species avoided parasitizing mature males of their hosts, probably for different reason. Mature male *N. clavipes* are probably too small to produce an adult *H. robertsae* (Fincke et al. 1990). Mature males of

P. argyra were, in contrast, not too small to produce adult wasps. For instance one moderately small mature male spider weighed 14.0 mg, somewhat more than the 13.7 mg of a parasitized penultimate male and 12.1 mg of a parasitized antepenultimate male. Mature male *P. argyra* were only parasitized about a tenth as often as mature females, however (totals of 5.1% of 136 males and 51.8% of 328 females in the two years). It was clear that both of the mature males parasitized in 2000 had been attacked when they were in the penultimate instar, because part of the cuticle from the previous instar adhered to the male's abdomen at the feeding scar below the larva in both cases.

The reason for lower parasitism of mature males was presumably either because female *H. argyraphaga* rejected mature male spiders, or were less able to find and attack them. Active rejection seems likely, because mature males of *P. argyra* often chase off smaller individuals and use their orbs to capture prey (10 of 11 males checked for this detail were at the hubs of an orb). Thus mature males are probably often exposed to hunting female wasps. Active avoidance of males may be advantageous to the wasps because at least sometimes mature males fail to construct a cocoon web (Eberhard in prep.), thereby probably making the wasp's cocoon more vulnerable to enemies.

The mating system of *H. argyraphaga* apparently differs from that of at least some other ichneumonids in which males are attracted to sites where females are emerging. Males of *H. argyraphaga* were apparently not attracted to emerging or recently emerged females as they rested on their cocoons, but quickly approached females after they flew to nearby vegetation. Females probably actively release a long-range attractant pheromone. Males appeared to concentrate their searching behavior at the tips of leaves of prominent plants, suggesting that they also use visual stimuli. The very short copulation of *H.*

argyraphaga was similar to that observed (in captivity) in *Schizopyga podagrica* (Nielsen 1935).

One possible difference between *H. argyraphaga* and *H. robertsae* is that the latter apparently does not induce the spider to spin a highly modified cocoon web. Perhaps induction of behavioral changes has been lost, as the larger size of *Nephila clavipes* and the corresponding greater durability of the mesh lines near its orbs (which often remain more or less intact for several days without repair by the spider—W. Eberhard unpub.) may make a modified web to support the cocoon unnecessary. Another possibility is that modification of spider behavior is a relatively recently derived character in *H. argyraphaga*, but the probable plesiomorphic status of this species within *Hymenoepimecis* (Gauld 2000) and the ability of *H. tedfordi* to modify the behavior of *L. mariana* (W. Eberhard, in prep.) argue against this idea.

Neither Bignell (1898) nor Nielsen (1923) mention modified spider webs in most of the polysphinctine larvae they studied, but Shaw (1994:125) states that "many spiders about to succumb to polysphinctines seek a concealed site into which they spin themselves". Nielsen (1923) noted that the last web that the host *Cyclosa conica* (Pallas) made before pupation by *Polysphincta nielseni* Roman was unusually small, and that such small orbs were especially resistant to damage. In contrast, he noted an apparently normal web of a "certain *Theridia*" with the cocoon of a *Acrodactyla degener* (Haliday) (Nielsen 1923). The web of the theridiid "*Theridion*" with the cocoon of a *Zatypota albicoxa* that he figured (Nielsen 1923) also seems normal, while Jimenez (1987) states that *Zatypota* sp., which parasitizes *Theridion contreras*, attaches its cocoon to the substrate rather than suspending it in the web. I have seen the cocoon of an unidentified species of *Zatypota* in an apparently unmodified web of its theridiid host, *Ane-losimus* sp. These sparse data thus suggest

the preliminary conclusion that the non-orb webs in which these wasps pupate are not modified. A possible variation is *Polysphincta tuberosa* Gravenhorst, which parasitizes the orb weaver *Araneus quadratus*; but, judging from the figure of the cocoon and an accompanying web (Nielsen 1923), this species may pupate in the silk retreat made by the host (Jones 1983) rather than on the orb. Much more work remains to clarify the evolution of the ability of these larvae to manipulate host web spinning behavior.

The failure of female *H. argyraphaga* to use the ovipositor for oviposition resembles oviposition in aculeate wasps. Similar, presumably convergent oviposition direct from the genital opening has been seen in an unspecified adelognathine ichneumonid, and is suspected in the braconid *Histeromerus* (Shaw 1995). The ovipositor of *H. argyraphaga* also injected paralyzing venom into the spider host, and the attacking wasp probably stabs the spider with her unsheathed ovipositor during the instant she is landing and seizing it. In addition, the ovipositor was used to pry eggs and larvae of previous females from the spider's abdomen, and may also be used to sting these larvae. Live larvae are difficult to pry from the spider. One of the distinguishing traits of Polysphinctini in general is a very sharply pointed ovipositor (Fitton et al. 1988). It is tempting to suppose that the sharp point is an adaptation to aid rapid penetration and immobilization of spider hosts, which are potentially dangerous hosts.

Most European polysphinctines appear to oviposit at rather consistent sites on their hosts (Shaw 1998), but extensive descriptions of intra-specific variation in oviposition sites on their host (e.g., Fig. 3) are not available for other polysphinctines, so it is not clear whether the substantial variation in *H. argyraphaga* is unusual. It is possible that selection to escape infanticide by subsequent females favors variation in where eggs are placed on the spi-

der. The larger larvae won out over smaller individuals in two cases in which two larvae grew on the same host.

Selection on spiders.—The success of attacks by *H. argyraphaga* depended on the wasp grasping the spider through the web as it rested at the hub of its orb. Both the spider's observed defensive behavior (dropping quickly on a drag line below the orb in response to the wasp's approach from above), and the circumstances in which some wasp attacks failed (when the wasp hit the orb too far from the spider to grasp it) support the old idea that meshes of lines associated with orb webs function to defend the spider from enemies (summaries in Lubin et al. 1982, Eberhard 1990). The strategy of attacking the spider from above functions well with the more or less horizontal orbs of *P. argyra*, but leaves the wasp unable to follow the spider down its drag line when it drops, as Bignell (1898) observed an unidentified polysphinctine to do by walking down the line.

This limitation on wasp attacks makes it difficult to explain why late instar and mature female *P. argyra* seldom spin a mesh above or below the orb. Such meshes often occur in the web of earlier instars of this species. Among 31 webs of as many adult females, 90% lacked any mesh above the orb, while the corresponding frequency for 52 penultimate nymphs was 65% ($p = 0.05$ with χ^2). Unpublished data from student projects strongly suggest that spiders build such meshes even more frequently in earlier instars. The phylogeny proposed for *Plesiometa*, *Leucauge*, and related genera (Hormiga et al. 1995) suggests that mesh construction is a derived trait in these two genera.

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Molecular Confirmation of Host Records for Ichneumonoid Parasitoids of Wood-boring Beetle Larvae

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Abstract.—Field observations in Sabah of a large braconine wasp, *Shelfordia* sp., investigating and ovipositor-probing at a frass hole in an exposed tree root suggested the possible location of a host. Investigation of the substrate revealed a paralysed and partly consumed larva of an anthribid beetle that had a 1st instar parasitic wasp larva on it. Both adult and larval wasps were sequenced, in separate laboratories, for the D2-D3 expansion region of the nuclear 28S rDNA gene. The sequences were identical and consideration of their unique features compared with many other sequences from ichneumonoids leads to confirmation that the hosts of *Shelfordia* spp. include Anthribidae living in tree roots. The implications of DNA sequencing for constructing quantitative food webs are discussed.

Host records for parasitic Hymenoptera are notoriously unreliable as has been well documented by Shaw (1994) and Noyes (1994). Errors in the literature derive from several sources including misidentification of the parasitoid, misidentification of the host, misidentification of both, and through the wrong association of a parasitoid with a putative host because of contamination of the rearing system. These problems are particularly true for concealed hosts such as wood-borers, gall makers, etc., because these substrates can contain many potential host species apart from the one that may be the focus of attention. Simply rearing a parasitoid and a potential host from a given piece of substrate has consequently often led to incorrect conclusions about what is parasitising what. Although it is sometimes possible carefully to dissect substrate and to identify any host and parasitoid remains, or to isolate and rear the host and its parasitoid in isolation, these are both difficult pro-

cedures requiring much skill and at least some luck. The development of molecular techniques, in particular DNA sequencing, has opened new and in some respects easier ways to solve these problems.

The braconine genus *Shelfordia* Cameron is relatively common from India, through the Indo-Australian Region, to N.E. Australia, often being found in local collections, no doubt because its species are rather large by parasitic wasp standards. Its identification has not been without problems though, and since its original description (Cameron 1902), nothing had been published on it under that name until it was discovered to be a senior synonym of *Sigalphogastra* Cameron (Quicke 1982). The genus name *Sigalphogastra* had, however, been very inconsistently applied, and few of the older publications citing this name (Shenefelt 1978) actually refer to taxa congeneric with the type species. In 1984, Quicke described a new genus *Rostraulax*, based on a species similar

to *Shelfordia sensu stricto*, but which had an elongate labio-maxillary complex and partly fused apical flagellomeres (Quicke 1984a). Although *Rostraulax* is recognisable by these autapomorphies, *Shelfordia* is, as far as we can tell at present, left paraphyletic with respect to *Rostraulax*, and the latter was formally synonymised with *Shelfordia* by van Achterberg (1993). Prior to now, there have been no available host data for the genus *Shelfordia*, although the especially long ovipositor of one Indian species, *S. longicaudata* van Achterberg, suggests that it is potentially a parasitoid of a host living deeply within wood (van Achterberg 1993). Since its original description, some 35 species have been reclassified into it (or its synonym, *Rostraulax*) (Quicke 1983, 1984b, 1985, 1988, 1991, Quicke and van Achterberg 1990, Quicke and Koch 1990, van Achterberg 1993, van Achterberg and O'Toole 1993), of which 11 are from the island of Borneo, all from Sarawak. No species-level keys are available for *Shelfordia*, and proper taxonomic revision is required before the species referred to here can be properly identified.

FIELD OBSERVATIONS

In August 1999, DLJQ and NML had the opportunity to collaborate with the group of Dr Maryati Mohamed of the Tropical Biodiversity and Conservation Unit, Universiti Malaysia, Sabah, and to observe some large braconid wasps in lowland tropical rain forest at Poring (Kinabalu National Park). Along a short stretch of one popular forest trail, some six or seven conspecific females of the large, entirely tropical, braconine wasp genus *Shelfordia*, were seen flying or sitting on low vegetation over a period of several days. As no host records are known for this genus we decided to observe them to see what they were attacking. Large braconine wasps are typically thought to be parasitoids of wood-boring beetle or lepidopteran hosts, and a large dead tree with abundant signs of borer activity nearby seemed to be the obvious place for them to

be searching. However, after several hours of observation, the wasps were never seen near this tree, but only near the path. The wasps were very cautious; they remained stationary on the low vegetation for long periods, and were easily disturbed by tourists passing by. After some while, however, we observed one and then another fly to land on a small (approximately 5cm diameter) tree root that was partially exposed by the path. Again the wasps remained stationary for about 20 minutes when one of them approached a boring from which fresh-looking wood particles were exuded. After antennating the site for several minutes, she raised her metasoma and probed into the frass hole with her ovipositor and sheathes. After a few moments she was observed making marked twisting movements with the apex of her metasoma and she was then collected.

METHODS

Collection.—The apparently-ovipositing adult female *Shelfordia* was collected with a net and placed into a clean vial containing 95% ethanol. Other adult wasps referred to in this paper were collected in the same way or in Malaise traps containing 95% ethanol. The tree root with frass hole was dissected the same day with a saw, hammer and chisel, and a boring located below the frass hole which contained a paralysed and partly deflated beetle larva upon which was a single small (<1mm long) parasitoid larva. The beetle and parasitoid larvae were handled with watch-makers' forceps and transferred to a clean tube with 100% ethanol.

Laboratory protocols.—For adult insects, DNA was extracted in the U.K. from single individuals stored in 100% ethanol by incubation at 37°C in Proteinase K for approximately 18 hours, followed by sodium acetate/ethanol precipitation and re-suspension in 20µl TE buffer. PCR reactions were carried out in 50µl volumes containing 0.5µl DNA extract, 0.5µl Boehringer Taq, 1.25 µl 20µM primer, 1.25 µl 10mM

dNTPs and 5 µl buffer. PCR conditions were 30 cycles of 98°C denaturation (15 seconds), 48°C annealing (30 seconds) and 72°C extension (40 seconds) with an initial denaturation of 3 minutes at 93°C and a final extension of 3 minutes. PCR products were purified with Pharmacia Amersham PCR purification kit and then sequenced directly using *Amplitaq FS* on an ABI 373 automated sequencer.

The parasitoid larva was stored in 95% ethanol and DNA extraction and sequencing was carried out in Helsinki. The larva was dried and ground in 50 µl TNE-buffer (1 M Tris, 5 M NaCl, 0.5 M EDTA) and 1 µl proteinase K (Sigma Chemical Co.). The samples were then incubated at 37°C overnight, followed by sodium acetate and ethanol precipitation, and resuspension in 20 µl TE-buffer (as TNE but without NaCl). PCR reactions were carried out in 50 µl volume reactions, 5 µl 10× Buffer II (Perkin-Elmer), 5 µl of 25 nM MgCl₂, 2 µl 10 µM primer, 3 µl of 10 nM dNTP, 0.25 µl *Amplitaq* DNA Polymerase, 31.75 µl H₂O and 1 µl DNA template. PCR conditions after an initial denaturation at 94°C (2 min), were denaturation at 96°C (15 s), annealing at 55°C (30 s), extension at 72°C (1 min) for 35 cycles and a final extension 72°C (7 min).

The larval PCR product was purified using Nucleospin PCR Purification kit and then sequenced in both directions using Big Dye terminators on an automatic sequencer ABI PRISM 377 (Perkin-Elmer).

The beetle larva was identified as an anthribid by reference to Lawrence and Britton (1991). Specimens are deposited in The Natural History Museum, London. Full DNA sequences are in the EMBL/GenBank/DDBJ databases; accession numbers AJ231540, AJ231541 and AJ277499-AJ277504.

RESULTS

The parasitoid larva and the putatively conspecific *Shelfordia* adult produced identical sequences for the 480 base pair length

of the D2 region that was readable for both (the small larva gave a weak sequence). These sequences were aligned by eye to each other and to those of a range of other S.E. Asian Braconinae, including a similarly-sized species of the related genus *Diamblomera* Enderlein, collected in a similar site approximately 150 meters away (Quicke *et al.* 2000), and several other braconines from Poring. Part of the alignment is shown in Figure 1, in which several features that are shared by both the female *Shelfordia* and the parasitoid larva found are indicated in bold italics.

DISCUSSION

The present findings of an identical 28S D2 DNA sequence for both the adult *Shelfordia* and the parasitic wasp larva found on its anthribid host (Fig. 1) can only be considered in the light of our knowledge of interspecific variation of this gene region within the Braconidae, and more precisely, the Braconinae. In the laboratory at Silwood Park, this gene region has been sequenced for more than 250 species of Braconidae and for 98 species of Braconinae (Belshaw *et al.* 1998, in preparation). On no occasion were any two species found to have identical sequences, even congeneric species always differing by at least two or three bases, and often by the presence of species-specific insertions or deletions (the above-mentioned Braconinae data set includes 7 species each of *Digonogastra* Ashmead and of *Bracon* Fabricius). Note also that there are several differences between the sequences of the two *Nesaulax* Roman species from Sabah sequenced (Fig. 1). Contamination of the samples is considered highly improbable because the specimens were not handled by the same equipment, were placed in separate clean vials, and DNA extraction and sequencing was carried out in different countries. This study emphasises the potential for the use of DNA sequence technology for making firm parasitoid/host associations that would not otherwise

ShelfordiaAD	TAATTGTAAGATGTTGTGCGCGTGCACTTCTCCCCTAGTAGGACGTCGCGACCCGT
ShelfordiaLA	TAATTGTAAGATGTTGTGCGCGTGCACTTCTCCCCTAGTAGGACGTCGCGACCCGT
DiablomeraS	TAATTGTAAGATGTTGTGCGCGTGCACTTCTCCCCTAGTAGGACGTCGCGACCCGT
Nesaulax sp 1	TAATTGTAAGATGTTGTGCGCGTGCACTTCTCCCCTAGTAGGACGTCGCGACCCGT
Nesaulax sp 2	TAATTGTAAGATGTTGTGCGCGTGCACTTCTCCCCTAGTAGGACGTCGCGACCCGT
Pachybracon	TAATTGTAAGATGTTGTGCGCGTGCACTTCTCCCCTAGTAGGACGTCGCGACCCGT
Nedinoschiza	TAATTGTAAGATGTTGTGCGCGTGCACTTCTCCCCTAGTAGGACGTCGCGACCCGT
Cratobracon	TAATTGTAAGATGTTGTGCGCGTGCACTTCTCCCCTAGTAGGACGTCGCGACCCGT
Hybogaster	TAATTGTAAGATGTTGTGCGCGTGCACTTCTCCCCTAGTAGGACGTCGCGACCCGT
ShelfordiaAD	TGAGT TTTTT GTT--GGTCTACGGCCCAAGTGGAGCTTTTAAT AAATT -----
ShelfordiaLA	TGAGT TTTTT GTT--GGTCTACGGCCCAAGTGGAGCTTTTAAT AAATT -----
DiablomeraS	TGAAT-----GTT--GGTCTACGGCCCAAGTGGTAGCTTTTAGTGAATT-----
Nesaulax sp 1	TGAGT-----GTTTCGGTCTACGGCCCAAGTGGAGCTTTTAATGAATT-----
Nesaulax sp 2	TGAGT-----GTTTCGGTCTACGGCCCAAGTGGAGCTTTTAATGAATG-AATT-
Pachybracon	TGAGT-----TGTT--GGTCTACGGCCCAAGTGGAGCTTTTAATGAATT-----
Nedinoschiza	TGAGT-----GTT--GGTCTACGGCCCAAGTGGAGCTTTTAGTGAATGAAATTT
Cratobracon	TGAGTAC----GTT--GGTCTACGGCCCAAGTGGTAGCTTTTAATGAATA-----
Hybogaster	TGAGT-----TGTT--GGTCTACGGCCCAAGTGGGAGcTTTAATGAATT-----
ShelfordiaAD	TTATTTATT AAAAA -CCCTTGGTGTT---TCCTGACTGGCACTCGTCGGTAT ATAC
ShelfordiaLA	TTATTTATT AAAAA -CCCTyGGTGTT---TCCTGACTGGCACTCGTCGGTAT ATAC
DiablomeraS	TTATTCATTGAAAA-CCCTTGGTGTT---TCCTGACTGGCACTCGTCGGTAT-T-C
Nesaulax sp 1	TTATTTATTGAAAA-CCCTTGGTGTT---TCCTGACTGGCACTCGTCGGTAT-T-C
Nesaulax sp 2	TTATTTGTTGAAAA-CCCTTGGTGTT---TCCTGACTGGCACTCGTCGGTAA-T-C
Pachybracon	TTATTCATTGAAAA-CCCTTGGTGTT---ACCTGACTGGCACTCGTCGGTAT-T-C
Nedinoschiza	TTATTCATTGAAAA-CCCTTGGTGTT---TCCTGACTGGCACTCGTCGGTAT-T-C
Cratobracon	TTATTCATTGAAAA-CCCTTGGTGTTGTTTCCTGACTGGCACTCGTCGGTAT-T-C
Hybogaster	TTATTCATTGAAAAACCcTTGGTGTT---TCCTGACTGGCGCTCGTCGGTAT-T-C
ShelfordiaAD	ATATGGTATTGA ---GCCGCAT-TA-ATTA---TATGCGTCTAT--ATCTGTGCGC
ShelfordiaLA	ATATGGTATTGA ---GCCGCAT-TA-ATknnnnnnnnnnnnnnnnnnnnnnnnnnnnnn
DiablomeraS	GTATGGTATTGA---GCCGCAT----ATTA---TATGCGTTCAT--ATCTGTGCGC
Nesaulax sp 1	GTATGGTATTGATCAGCCGCAT----ATTA---TATGCGTTCGT--ATCTGTGCGC
Nesaulax sp 2	GTATGGTATTGA---GCCGCAT----ATTA---TATGCGTCCAAATATCTGTGCGC
Pachybracon	GTATGGTATTGA---GCCGCATAT--ATTA---TATGCGTTCAT--ATCTGTGCGC
Nedinoschiza	GTATGGTATTGA---GCCGCATATATATTA---TATGCGTTCAT--ATCTGTGCGC
Cratobracon	GTATGGTATTGA---GCCGCA----ATTATATATATGCGTCCAT--ATCTGTGCGC
Hybogaster	GTATGGTATTGA---GCCGCAC----ATTA---ATATGCGTCCTT--GTCTATCGC

Fig. 1. Manually aligned 28S D2 rDNA sequences including adult of the *Shelfordia* found probing the anthribid burrow (*Shelfordia*AD), the larva found on the anthribid beetle larva (*Shelfordia*LA), other braconines from Poring (*Diablomera* sp., *Nesaulax* spp 1 and 2 and *Pachybracon* sp.), and other large braconine wasps from the Island of Borneo. Bases unique to the *Shelfordia* female and the putatively conspecific parasitoid larva are indicated in **bold italics**.

be possible. Although DNA-based techniques have been used to detect parasitoid larvae inside their hosts (e.g., Greenstone and Edwards 1998), and similar results have been obtained recently for predatory insects using traces of prey DNA remaining in the predator's gut in a well characterised predator-prey system (Agusti *et al.* 1999), DNA has not yet been used 'blind' to determine hosts or prey in open systems. We show here that DNA sequence data, in combination with a data base of sequences of related taxa, has the potential to greatly facilitate studies not only on the autecologies of particular

hosts through providing data on their parasitoids, but also to allow construction of fully quantitative food webs (e.g., Memmott and Godfray 1993). In this latter case, it also opens up the possibility of working on groups that are notoriously difficult to rear in isolation such as species that consume rotting wood and their parasitoids. With the addition of order-specific primers, it should also be possible to discover and identify endoparasitoids.

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The Venezuelan Species of *Pimpla* (Hymenoptera: Ichneumonidae)

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Abstract.—The Venezuelan species of *Pimpla* (Hymenoptera: Ichneumonidae: Pimplinae) are reviewed. Four new species are described and illustrated: *P. lasallei*, *P. mitchelli*, *P. vangeli* and *P. vayonae*. An identification key to 18 species is given, including the previously described species: *P. albomarginata* Cameron, *P. azteca* Cresson, *P. bolivari* Porter, *P. caeruleus* Cresson, *P. croceipes* Cresson, *P. croceiventris* (Cresson), *P. flavipennis* Enderlein, *P. ichneumoniformis* Cresson, *P. platysma* Porter, *P. punicipes* Cresson, *P. pyramis* Porter, *P. sanguinipes* Cresson, *P. sumichrasti* Cresson and *P. tomyris* Schrottky. *Pimpla croceipes*, *P. croceiventris*, *P. ichneumoniformis*, *P. pyramis* and *P. tomyris* are recorded for the first time in Venezuela.

Pimpla is a large genus represented in almost all regions of the world, although it does not seem to be present in Australia and New Zealand (Gauld 1984, Gupta 1987). The species of *Pimpla* are idiobiont parasitoids of lepidopterous pupae and prepupae. Terán (1980) recorded the following host associations from Venezuela: *P. azteca* from a pupa of *Alabama argillacea* (Noctuidae); *P. platysma* from a pupa of *Antichloris eriphia* (Syntomidae); *P. punicipes* from *A. argillacea*, *Oiketicus* sp. and *Platoteeticus* sp. (Psychidae), and *Phobetron hipparchia* (Eucleidae); *P. sumichrasti* from a pupa of *Hypsipylla grandella* (Pyrilidae).

Townes and Townes (1966) recorded 29 species as occurring in the Neotropics, but only *P. albomarginata*, *P. punicipes* and *P. sanguinipes* were cited from Venezuela. Porter (1970) conducted the first taxonomic study of the South America members of the genus. He treated 35 species, of which 21 were described as new. Only *P. bolivari* was described as new from Venezuela and *P. caeruleus* was recorded for the first time in this country. Gauld (1991) treated 17 Costa Rican species of which 8 are present in Venezuela. These last two works must be seen for a detailed review of the infor-

mation available on biology, etology and host preferences.

MATERIALS AND METHODS

Species treated in this study were identified using the keys of Porter (1970) and Gauld (1991) or through comparison with material examined in The Natural History Museum (British Museum) in 1996. Approximately 800 specimens of *Pimpla* were examined. The following institutions provided specimens for this study:

BMNH: The Natural History Museum, London, U.K.

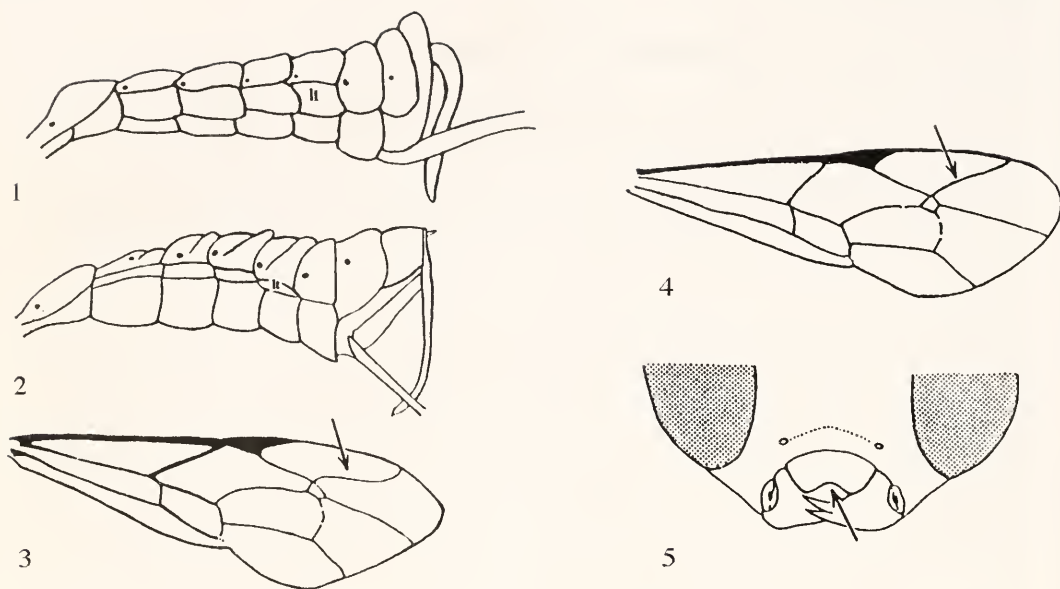
MIZA: Museo del Instituto de Zoología Agrícola, Facultad de Agronomía, Universidad Central de Venezuela, Maracay, Venezuela.

UCOB: Museo Dr. J. M. Osorio, Departamento de Ciencias Biológicas, Agronomía, Universidad Centroccidental Lisandro Alvarado, Tarabana, Lara, Venezuela.

The nomenclatural treatment, morphological terminology and taxonomic characters used here follow the work of Gauld (1991). Microsculpture terminology follows that of Eady (1968).

KEY TO VENEZUELAN SPECIES OF *PIMPLA*

- 1. Metasoma with laterotergite V broad, more than 0.5 times as broad as long (Fig. 1); malar space wide, as long as or longer than basal mandibular width, that of male more than 0.7 times basal mandibular width 2
 - Metasoma with laterotergite V narrow, less than 0.3 times as broad as long (Fig. 2); malar space narrow, less than 0.75 times as long as basal mandibular width, that of male less than 0.6 times basal mandibular width (in *P. flavipennis* is more than 1.0 times basal mandibular width) 3
- 2. Laterotergites II and III more than 0.5 times as broad as long, of similar width to laterotergites IV and V (Fig. 1); female with posterolateral corner of mesopleuron usually finely punctate; male hind tibia with central white band *punicipes* Cresson
 - Laterotergites II and III less than 0.3 times as broad as long, clearly narrower than laterotergites IV and V (Fig. 2); female with posteroventral corner of mesopleuron striated; male hind tibia reddish *sanguinipes* Cresson
- 3. Forewing with Rs strongly sinuous (Fig. 3); tergite I of female rather slender, in profile evenly convex 4
 - Forewing with Rs more or less straight (Fig. 4); tergite I of female short and broad, in profile generally strongly convex 10
- 4. Head and mesosoma predominantly yellow or orange, sometimes with black marks, forewing with an apical black spot 5
 - Head and mesosoma predominantly black or blackish brown; forewing without apical black spot 7
- 5. Mesoscutum entirely yellow or orange 6
 - Mesoscutum yellow with three longitudinal black stripes; female with tergites VI and VII of metasoma almost entirely black *sumichrasti* Cresson
- 6. Metasoma predominantly orange, at most with only extreme anterior margins of tergites I-IV black; propodeum smooth and polished *azteca* Cresson
 - Metasoma predominantly yellow; female with tergites VI and VII of metasoma wholly black; propodeum with several strong transverse wrinkles *mitchelli* sp.n
- 7. Metasoma black with extensive yellow marks 8
 - Metasoma black without yellow marks, sometimes apical margins of tergites with a brownish tinge 9
- 8. Ovipositor very strongly flattened beyond basal 0.5; mesopleuron without wrinkles in posteroventral corner *platysma* Porter
 - Ovipositor stouter and not strongly flattened; posteroventral corner of mesopleuron with some wrinkling *tomyris* Schrottky
- 9. Antenna brownish; forewing yellowish with entire anterior margin strongly infumate; basal 0.5 of tergite I closely and coarsely punctate *ichneumoniformis* Cresson
 - Antenna black; forewing uniformly yellow; tergite I almost wholly smooth *flavipennis* Enderlein
- 10. Apex of clypeus deeply bilobed (Fig. 5); forewing with cu-a slightly distal to the base of Rs & M 11
 - Apex of clypeus slightly concave; fore wing with cu-a opposite to the base of Rs & M 16
- 11. Mesoscutum entirely black; propodeum without conspicuous posterolateral tubercles ... 12
 - Mesoscutum black with white marks; propodeum with conspicuous posterolateral tubercles 14
- 12. Tergite I in profile with high, more or less sharply pyramidal hump; all coxae black; mesopleural suture strongly foveolate *pyramis* Porter
 - Tergite I in profile with moderately high blunt hump; coxae without black markings; mesopleural suture weakly foveolate 13
- 13. Sternite I with strongly produced swelling, postscutellum black; fore coxa white; metasoma black and white banded *albomarginata* Cameron



Figs. 1-5. *Pimpla*. 1-2, Metasoma, lateral view, showing laterotergites (lt): 1, *P. punicipes*; 2, *P. sumichrasti*. 3-4, Fore wing: 3, *P. sumichrasti*; 4, *P. lasallei*. 5, *P. lasallei*. Clypeus, anterior view.

- Ventral swelling on sternite I rather low and rounded; postscutellum pale yellow; forecoxa pale yellow; metasoma black and white with reddish-brown tinge that becomes stronger on tergites VI and VII *bolivari* Porter
- 14. Ovipositor stout; tergites VI and VII reddish with apical margins yellowish; sternite I yellowish-brown *lasallei* sp.n
- Ovipositor thin and short; tergites VI and VII black and white banded or uniformly reddish; sternite I black 15
- 15. Tergite I short, almost as long as apical width; propleuron with two white marks; hind tibia black with premedial white band *vayonae* sp.n
- Tergite I 1.5 times as long as apical width; propleuron wholly black; hind tibia reddish, its extreme base black and premedial band yellow *vangelii* sp.n
- 16. Body metallic blue, wings blackish; male with forecoxa white marked anteriorly *caerulea* Cresson
- Body not metallic, head and mesosoma black, wings hyaline 17
- 17. Metasoma and hind coxa uniformly black; hind tibia bright yellow *croceipes* Cresson
- Metasoma and hind coxa reddish; hind tibia orange *croceiventris* (Cresson)

Pimpla mitchelli Díaz, new species

Holotype female.—Forewing length 13.5 mm. Head in dorsal view moderately short, with genae rounded behind eyes; frons strongly concave; posterior ocellus separated from eye by diameter of ocellus. Mandibles moderately long, strongly and evenly tapered, with upper tooth approx-

imately 1.6 times the length of lower tooth; clypeus in profile weakly convex basally, apically flat; clypeus in anterior view 2.5 times as wide as medially long, with apical margin very slightly concave; malar space 0.4 times as long as basal mandibular width; lower face centrally weakly convex, smooth and shining, with

few irregularly dispersed punctures under the antennal sockets. Mesoscutum polished, with fine punctures separated by about $1.0\times$ their diameter; weakly convex; scutellum polished with few dispersed fine punctures separated by about $1.5\times$ their diameter. Mesopleuron highly polished, with few and sparse punctures separated by about $3.0\times$ their diameter, posterodorsally smooth; epicnemial carina reaching above level of centre of pronotum; metapleuron convex, smooth and polished, with punctures only along its upper margin; submetapleural carina strongly raised in anterior part, evanescent in posterior 0.4 of metapleuron. Propodeum in profile rounded; pleural carina absent; anterior 0.5 of the dorsal surface with several strong transverse wrinkles, posterior 0.5 smooth. Forewing with distal abscissa of Rs strongly sinuous; cu-a distal to base of Rs & M by 0.2 times its own length; discosubmarginal cell densely setose; abscissa of Cul between 1m-cu and Cu1a as long as Cu1b. Tergite I of metasoma short and stout, almost as long as apical width, smooth; tergite I in lateral view with dorsal surface weakly convex; sternite I not clearly swollen centrally; tergite II highly polished, with dispersed punctures in anterior part, punctures separated by about $1.5\times$ their diameter, posterior part smooth, anterolaterally with well-defined oblique grooves; tergites III-V similar, but with oblique grooves progressively weaker on succeeding segments; laterotergites II-V narrow and inconspicuous, less than 0.2 times as broad as long. Ovipositor sheath 0.8 times as long as hind tibia; apex of ovipositor subcylindrical, with upper valve smooth and lower valve with 7 ridges that do not extend laterally. Color: Predominantly orange. Mandibular teeth, small D-shaped spot between posterior ocellus and eye, small triangular spot under median ocellus, scape and pedicel dorsally, flagellum, scuto-scutellar sulcus, tergite VI, and most of tergite VII, black. Posterior half of tar-

somere I of foreleg, tarsomeres 3–5 of middle leg, hind tarsus except basitarsomere, apical half of hind tibiae, two rounded spots in the middle of tergite I, anterior margin of tergite II-V and posterior margin of tergites I-V, dark brown to blackish. Wings with slight yellow tinge and with distinct subapical blackish spot. Pterostigma yellow.

Etymology.—This species is dedicated to Pam Mitchell for her generosity and her contribution to the study of Neotropical Ichneumonidae.

Remarks.—*P. mitchelli* belongs to the *sumichrasti* species-group. It differs from *P. sumichrasti* in having the mesoscutum, mesopleuron, propodeum, and mid and hind coxae orange. It differs from *P. azteca* and the Central American species *P. personi* in the coloration of the metasoma. The only specimen at hand was collected with a net. Nothing is known about its biology.

Material examined.—Holotype ♀, Venezuela, Bolívar State, Caicara- San Juan de Manapiare road, km 210, 30. m, iv-1976 (Gélvez & Salcedo) (MIZA).

Pimpla lasallei Diaz, new species

Holotype female.—Forewing length 12 mm. Head in dorsal view moderately short, with genae reduced behind eyes; frons strongly concave; posterior ocellus separated from eye by 0.6 times diameter of ocellus. Mandible of moderate length, strongly and evenly tapered, with upper tooth 1.5 times length of lower; clypeus basally moderately convex, apically flattened; clypeus in anterior view 1.7 times as broad as medially long, apically bilobate; malar space 0.8 times as long as basal mandibular width; lower face centrally weakly convex, shallowly and closely punctate, punctures separated by about $0.5\times$ their diameter. Mesoscutum slightly polished, shallowly punctate, punctures separated by about $0.5\times$ their diameter; scutellum convex, smooth. Mesopleuron slightly polished, with punctures separated by about $1.0\times$ their diameter, epicne-

mial carina reaching above level of centre of pronotum; metapleuron moderately convex, coarsely striate; submetapleural carina complete, anteriorly raised. Propodeum in profile moderately declivous, posterolateral tubercles slightly pointed; pleural carina incomplete; dorsal surface of propodeum centrally strongly striate, striae crossing tubercles, anteriorly weakly striated, posteriorly smooth and polished. Forewing with distal abscissa of Rs straight; cu-a distal to base of Rs&M by less than 0.2 times length of cu-a; discosubmarginal cell with glabrous area along veins Rs&M, Cu 1 and 1 m-cu; abscissa of Cu 1 between 1 m-cu and Cu1a 1.8 times as long as Cu1b. Tergite I of metasoma moderately long, 1.7 times as long as apical width; tergite I in lateral view slightly convex, lateral carina distinct on spiracle. Sternite I moderately long, weakly swollen just behind its centre; tergite II smooth, with few irregularly sparse and shallow punctures, anterolaterally with deep oblique grooves. Tergites III-V similar, anterolateral grooves becoming progressively weaker; laterotergites III-V narrow and inconspicuous, 0.2 times as broad as long. Ovipositor sheath 0.6 times as long as hind tibia; apex of ovipositor depressed, the lower valve not laterally expanded. Color: Predominantly black. Clypeus brown-reddish. The following whitish-yellow: scape ventrally, palpi, upper and anterior margins of pronotum, propleuron, lateral margin of mesoscutum, narrow stripes along position of notauli that reach scutoscuteellar sulcus, scutellum, small crescentic spot on postscutellum, upper margin of tegula, subalar prominence, two elongate spots on epicnemium, antero-dorsal area of mesepisternum, circular spot on the lower-posterior part of mesepisternum, mesepimeron, drop-shaped spot on the upper area of metapleuron, propodeal tubercles, and posterior margin of tergites. Fore and middle legs yellowish, excepting for orange of dorsal area of femora. Hind coxa brown

with irregular D-shaped whitish spot on proximal end dorsally, trochanter and trochantellus yellow, femur brown, tibia with proximal end brown, its basal half yellowish and its apical half brown, tarsomeres orange, progressively darker. Wings with slight yellowish tinge. Pterostigma yellow-orange.

Male.—Similar to female but with fore wing length 8.3 mm; malar space 0.6 times as long as basal mandibular width; discosubmarginal cell with glabrous area only below pterostigma; color as female except that metapleuron and mesoscutum in front of tegulae without white spots.

Etymology.—This species is named in honor of John LaSalle for his studies on Neotropical Eulophidae and his spirit of friendly collaboration.

Remarks.—*P. lasallei* belongs to the *albomarginata* group. It is easily recognized by its large size, the strongly produced ventral swelling on sternite 1, and its color pattern.

Biological notes.—*P. lasallei* has only been found in Venezuela. Two specimens were taken with a net in a typical rain forest. No host records are available for this species.

Material examined.—Holotype ♀, Venezuela, Lara State, Yacambú National Park, La Pastora, 1600 m, III – 1981 (F. A. Díaz & C. Pereira) (UCOB). Paratype. Venezuela: Lara State, Yacambú National Park, 1 M, same data as holotype (UCOB).

Pimpla vayonae Diaz, new species

Holotype female.—Forewing length 7.3 mm. Head in dorsal view short, with genae constricted behind eyes; frons strongly concave. Posterior ocellus separated from eye by about 0.6 diameter of ocellus. Mandibles moderately long, evenly tapered, with upper tooth about 2.0 times length of lower; clypeus in anterior view 2.0 times as broad as medially long, apically strongly bilobate; malar space 0.8 times as long as basal mandibular width; lower face centrally weakly convex, with shallow

punctures separated by about $0.7\times$ their diameter. Mesoscutum shining with punctures separated by about $0.7\times$ their diameter; scutellum convex, smooth. Mesopleuron highly polished, ventrally with close punctures separated by about $1.5\times$ their diameter, dorsoposteriorly smooth; epicnemial carina reaching above level of centre of pronotum. Metapleuron moderately convex, dorsally with some striae and coarse punctures separated by about $1\times$ their diameter, ventrally with sparse fine punctures separated by about $2\times$ their diameter; submetapleural carina complete, raised anteriorly. Propodeum in profile weakly declivous, with strong and blunt tubercles posterolaterally; pleural carina only present anteriorly; dorsal surface of propodeum anteriorly transversely weakly wrinkled, area between tubercles smooth and shining. Forewing with abscissa of Rs straight; cu-a distal to base of Rs&M by 0.3 times its own length; discosubmarginal cell moderately setose, with setae more sparse toward margin of Rs&M; abscissa of Cu1 between 1m-Cu and Cu1a 1.6 times as long as Cu1b. Tergite I very short and stout, almost as long as apical width; tergite I in lateral view convex; sternite I short, strongly swollen just before its centre, with swelling directed forward. Tergite II microaciculate and shining, anterolaterally with deep oblique impressions; tergites III-V similar, with anterolateral furrows becoming progressively weaker. Laterotergites II-V narrow and inconspicuous, 0.2 times as broad as long. Ovipositor short and thin; ovipositor sheath 0.4 times as long as hind tibia; apex of ovipositor cylindrical. Color: Predominantly black. The following white: Ventral face of scape, palpi, upper and anterior margins of pronotum, two oval marks on propleurum, two triangular marks on anterior margin of mesoscutum which run backward along notauli, scutellum, post-scutellum, tegula, subalar prominence, anterodorsal area of mesepisternum, circular spot located just above middle coxa, me-

soepimeron, propodeal tubercles, posterior half of propodeum except area petiolaris, hind margin of all tergites. Foreleg with coxa except extreme base, trochanter, inner face of trochantellus, stripe along inner face of femur, apex of outer face of femur, and inner and outer faces of tibia white. Remainder of trochantellus, femur, and tibia, orange. Tarsus orange, tarsomere V darker. Middle leg with coxa white, except for orange dorsal face; trochanter, trochantellus, and femur orange; tibia with its basal 0.2 and apical 0.3 dark brown, its central part white; tarsus dark brown, tarsomere V blackish. Hind leg with coxa reddish, its dorso-anterior face with circular white mark; trochanter, trochantellus and femur, red; tibia black with a premedial white ring. Tarsus black. Wings hyaline. Pterostigma black with base and apex whitish.

Male.—Unknown

Etymology.—This species is named in honor of Venezuela Carrizo Ayona for her generosity and spirit of collaboration.

Remarks.—*P. vayonae* belongs to the *albomarginata* species complex, and is related to *P. vangeli* and the Mesoamerican *P. edgari* Gauld. All three species have the ovipositor short and thin. *P. vayonae* differs from *P. vangeli* and *P. edgari* in the coloration of propleurum, mesopleurum and hind legs, and in having tergite I almost quadrate and the propodeum weakly striated.

Biological notes.—*P. vayonae* has only been found in Venezuela. The specimen was collected in a Malaise trap situated in a coffee-Macadamia area. Nothing is known about its biology.

Material examined.—Holotype F. Venezuela: Lara state: Villanueva, Finca "Las Lomas", 900m. III-1994 (F.A.Díaz) (UCOB).

Pimpla vangeli Díaz, new species

Holotype Female.—Forewing length 9.3–9.6 mm. Head in dorsal view short, with genae constricted behind eyes; frons strongly concave; posterior ocellus sepa-

rated from eye by 0.4–0.6 times diameter of ocellus. Mandibles of moderate length, strongly and evenly tapered, with upper tooth 1.5–1.6 times length of lower; clypeus in profile moderately convex, apically flattened; clypeus in anterior view 1.6–1.7 times as broad as medially long, apically bilobate; malar space 0.7–1.0 times as long as basal mandibular width; lower face centrally weakly convex, with shallow punctures separated by $0.7\times$ their diameter. Mesoscutum slightly polished, with shallow punctures separated by about $0.5\times$ their diameter; scutellum convex, smooth. Mesopleuron weakly polished, evenly, finely and closely punctate, the punctures separated by $0.5\times$ their diameter; epicnemial carina reaching above level of centre of pronotum. Metapleuron convex, coarsely striate; submetapleural carina distinct, complete, anteriorly sharply raised. Propodeum in profile slightly inclivous, pleural carina present only anteriorly; dorsal surface of propodeum anteriorly transversely wrinkled, posteriorly with pair of strong and blunt tubercles, area between tubercles smooth and shining. Fore wing with distal abscissa of Rs almost straight; cu-a distal to the base of Rs&M by 0.3 times length of cu-a; discosubmarginal cell evenly and densely setose; abscissa of Cu1 between 1m-Cu and Cu1a 1.7–1.8 times as long as Cu1b. Tergite I of metasoma moderately short and stout, 1.5 times as long as apical width; tergite I in lateral view strongly convex; lateral carina present only posteriorly. Sternite I moderately long, strongly swollen just before its centre, apex of swollen area directed anteriorly. Tergite II microaciculate, weakly polished, anterolaterally with oblique grooves. Tergites III–V similar; laterotergites II–V narrow and inconspicuous, less than 0.2 times as broad as long. Ovipositor very short and thin; its sheath 0.4 times as long as hind tibia; apex of ovipositor depressed. Color: Predominantly black with clypeus and mandibles brown, palpi yellowish, apex of scape yellow-

low-brownish. The following white: Dorsal and anterior margins of pronotum, anterolateral margin of mesoscutum, narrow stripe along notauli, tegula, scutellum, subalar prominence, mesopleuron, propodeal tubercles, posterior half of propodeum and hind margin of tergites I–IV. Posterior half of tergite V and tergites VI and VII reddish. Foreleg with coxa white, its inner basal extreme blackish; trochanter whitish; trochantellum whitish except for orange inner face; femur, tibiae, and tarsus orange. Middle leg with coxa yellowish, its outer face orange, basal and apical extremes infuscated, rest of middle leg orange excepting for lighter premedial area of tibia. Hind leg with coxa reddish, its outer face with D-shaped whitish mark and its apex black; femur reddish with apex black; tibia reddish with its basal 0.1 black, and premedial area yellow, its outer face darker than inner face; tarsi dark brown. Wings weakly and evenly infuscated. Pterostigma blackish.

Male.—Similar to female but with fore wing length 8.1 mm, malar space 0.7 times as long as basal mandibular width, propodeal wrinkles weaker, tergite I longer and tergites II–VII with abundant setiferous punctures.

Etymology.—This species is named in honor of Angel Luis Vilorio (University of Zulia, Venezuela), for his dedication to the study of Satyridae (Lepidoptera) and for his unique concept of friendship and solidarity.

Remarks.—*P. vangeli* belongs to the *albomarginata* species complex. It can be easily distinguished by its short and thin ovipositor, the color of metasoma and hind legs and the wings evenly infuscated. Three specimens collected with a net are at hand. No details of the biology of this species are known.

Material examined.—Holotype O. Venezuela: Lara state: Rio Claro, 1200 m, v-1973 (J. M. Osorio and R. González) (UCOB). Paratypes: Venezuela. 1 female, Lara state, Sanare, 1350m, VII-1993 (A. J. Escalona) (BMNH). 1M, Lara state, 8 km SE Sanare,

La Capilla, 1800 m, II-1993 (F. A. Díaz) (UCOB).

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Family Group Names in Braconidae (Hymenoptera: Ichneumonoidea)

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Abstract.—The known family-group names for Braconidae are listed with their authors and dates of publication. The status of the 224 previously proposed names is reviewed, with particular attention to the validity and priority of names used by nineteenth century authors.

The family Braconidae is exceptionally diverse. It is the second largest family within the Hymenoptera, and contains over 15,000 described species. Considerable attention has been given to the classification of the Braconidae in recent years, including the production of comprehensive catalogs and regional synopses and the publication of several treatises on higher order relationships within the family (e.g., Shenefelt 1969, 1980, Fischer 1971, 1972, Čapek 1965, 1970, Mackauer and Starý 1967, Mackauer 1968, Tobias 1976b, 1986, Mason 1981a, 1983, van Achterberg 1984, Quicke and van Achterberg 1990, Shaw and Huddleston 1991, Wharton et al. 1992, 1997, van Achterberg and Quicke 1992). There have been numerous changes in the subfamily classification, and shifts in rank are commonplace. In the same year, for example, Sharkey (1993) and van Achterberg (1993) recognized 29 and 43 subfamilies, respectively, in the Braconidae. As subfamilies, tribes, and subtribes are either combined into larger units or split into smaller ones, it is essential to know which family-group names are available, and which have priority. The following discussion on available family-group names is therefore offered to facilitate the correct application of family-group names to braconid taxa. We welcome further discussion on this matter.

INTERNATIONAL CODES OF ZOOLOGICAL NOMENCLATURE

As noted by Menke (1997), there have been detailed presentations on how the Third Edition of the International Code of Zoological Nomenclature (ICZN 1985) applies to family-group names in other groups of Hymenoptera (Fitton and Gauld 1976, Michener 1986). The recently published Fourth Edition (ICZN 1999) contains only a few pertinent additions. We therefore present a brief discussion here, focusing of those provisions of particular relevance to the Braconidae. Some knowledge of the history of braconid classification relative to the development of various Codes or Règles is also necessary for a complete understanding of the rationale for earlier name changes. Prior to the publication of the 1961 version of the Code (ICZN 1961), for example, replacement of a family-group name was a standard and acceptable practice when its type genus was discovered to be a junior synonym. This practice was disallowed under the 1961 Code for names falling into synonymy after 1960. Nevertheless, some of the older replacement names have become well established in the Braconidae, and are still used today (Article 40.2).

Names not based on genera are not available (Article 11.7). This applies to the names used by Wesmael (1835) to group

genera within the Braconidae, names that were nevertheless adopted by most subsequent authors through the first half of the 20th century. A family-group name proposed after 1930 must also be accompanied by a statement of characters differentiating the group, or reference to same, or be a replacement name (Article 13). Though there are few such cases in the Braconidae, it is not always clear when these names have met the criteria for availability in subsequent publications. Article 13.2.1, a new section added to ICZN (1999), further complicates this problem.

Articles 35.4 and 40.2 apply to the authorship and dates of availability of family-group names affected by replacements for unjustified emendations or synonyms. We agree with Menke (1997) that the results are not particularly satisfying (since a name could then become available before the birth of its author), but we accept this, and have noted those cases below. Similarly, there are a few family-group names in the Braconidae that are invalid because the type genus is a junior homonym (Article 39).

ASSESSMENT OF RELEVANT LITERATURE

The works of Nees von Esenbeck (1812, 1814, 1816) represent the first attempt to establish a hierarchical framework for the Braconidae. Working in close association with Gravenhorst, who had just published his first significant monograph on the Ichneumonidae (Gravenhorst 1807), Nees concentrated on the "Ichneumonides adsciti," which contained the species now included in the Braconidae. In this series of papers (dated 1811–1813, but actually published from 1812–1816), Nees used the word "familia" to denote both groups of species within a genus as well as groups of genera. He also gave collective names to some of these groups of species and two of the groups of genera. The collective names used in this series of papers include

names later used to establish formal generic and suprageneric categories in subsequent papers (Nees von Esenbeck 1819, 1834). The collective names so used by Nees were Cheloni, Sigalphi, Microgasteres (-i), Agathides, Bracones, and Bassi. The first four names were clearly used in the sense of groups of species within a genus, though this is not apparent unless all three parts of the series are examined. The genus *Sigalphus* Latreille, for example, was divided into "Familia I. Sigalphi" (Nees von Esenbeck 1816, p. 247) and "Familia II. Cheloni" (Nees von Esenbeck 1816, p. 260). The 18 nominal species treated by Nees (1816) under his "Familia II. Cheloni" were all listed in binominal form with *Sigalphus* as the genus name. These four names thus do not satisfy Article 11.7.1.2 (ICZN 1999) for establishment of family group names. Nevertheless, there has been some confusion in this regard, with the subfamily names Agathidinae, Cheloninae and Microgastrinae variously attributed to Nees, Blanchard (1845) or Foerster (1862) over the past 30 years.

The names Bracones Nees von Esenbeck, 1812 and Bassi Nees von Esenbeck, 1812, however, were used in a hierarchical sense to denote suprageneric groups. The nominal genera included in Bracones were *Stephanus* Jurine, *Bracon* F., *Microgaster* Latreille, *Microdus* Nees, and *Agathis* Latreille (Nees von Esenbeck 1812, 1814). Nominal genera included in Bassi were *Bassus* Nees, *Eubazus* Nees, *Helcon* Nees, *Sigalphus*, and *Ichneutes* Nees (Nees von Esenbeck 1814, 1816). Bracones and Bassi are the oldest available family group names known to us for members of what is now the family Braconidae. The family name Braconidae can thus be attributed to Nees (1812). Bassinae Nees (available from Nees 1812, but not completely described until Nees 1814, p. 200) is unfortunately problematic, since it is based on *Bassus* Nees, 1814. Nees (1814) inexplicably proposed the name *Bassus* for *Alysia* Latreille, 1804, citing Latreille's *Alysia* on the line follow-

ing "*Bassus mihi*." Nees (1814) failed to cite the use of the name *Bassus* by Fabricius (1804), which, based on the accepted type species *Ichneumon calculator* F., 1798, belongs to the Agathidinae rather than the Alysiinae. While it is also possible that Nees simply misidentified *Bassus* Fabricius (following the interpretation of *Bassus* by Spinola (1808) and others), Nees (1814) nevertheless used the term "*mihi*" when describing *Bassus*, leading to uncertainty in the application of the name. The family group name Bassi is thus based on a junior objective synonym (of *Alysia*) as well as a junior homonym (of *Bassus* F.).

Nees (1819) eventually recognized *Alysia*, and later (Nees 1834) replaced the family group name Bassi with Alysioideorum. Earlier, however, Leach (1815) proposed Alysiada and Stephens (1829) proposed Alysiidae as family-group names for the species placed in *Alysia*. Thus, the subfamily name Alysiinae dates from Leach (1815), though it is often credited to Stephens (1829). Since the family group name Bassi was replaced well before 1961, and the replacement name has won general acceptance, Article 40.2 (ICZN 1999) would appear to apply, and Bassinae would therefore become a synonym of Alysiinae. Nevertheless, Article 39 (ICZN 1999) also applies, and Bassinae, based on a junior homonym, is thus invalid. If, however, *Bassus* Nees is treated as a misidentification of *Bassus* Fabricius, then Bassinae could be viewed as a senior synonym of Agathidinae. As stability would be affected in this case (by the resurrection of Bassinae after 163 years), Articles 41 and 65 (ICZN 1999) apply, and the matter would have to be referred to the Commission. As all internal evidence points to *Bassus* Nees as a separate taxon from *Bassus* F., it seems logical to treat Bassinae as invalid due to homonymy of the type genus.

The first three family-group names applicable to our current concept of the family Braconidae were thus proposed by Nees (1812) and Leach (1815). Several other early workers, some predating Nees,

presented classifications or arrangements of parasitic wasps in general or ichneumons in particular. Several adopted the names proposed by Nees (1812, 1814, 1834) and Leach (1815) to designate groups of genera, while others proposed additional names. Most of the newly proposed names in these early publications were not based on included genera and thus do not satisfy the requirements of the current Code of Zoological Nomenclature (ICZN 1999) for availability of family-group names. To our knowledge, only two other authors proposed valid, family-group names prior to the work of Foerster (1862). These were Haliday (1833b) and Blanchard (1845).

Haliday (1833a) presented an outline of his classification of the parasitic Hymenoptera of Britain, then filled in the outline with descriptions of the genera and species in subsequent issues of the Entomological Magazine. In a "Tabula Synoptica," Haliday (1833b) proposed a division of Nees' Ichneumones adsciti into 4 tribes: Aphidini, Sigalphini, Braconii, and Agathenses. The currently used family-group names Agathidinae, Aphidiinae, and Sigalphinae should therefore be attributed to Haliday (1833b). Haliday's proposal of valid family-group names is often overlooked because Haliday did not use these names in the remainder of his work, and later, Haliday (1840) unfortunately abandoned this arrangement in favor of the divisions used by Wesmael (1835). Wesmael's names (Cyclostomes, Areolaires, Polymorphes, and Cryptogastres), though unavailable from the standpoint of formal family-group taxa, were nevertheless widely used by subsequent authors well into the 20th century.

Blanchard (1845) was the next author to propose new family-group taxa in a manner consistent with the Code. Blanchard (1845) arranged the braconid genera known to him into six named groups. Four of these had already been proposed as family-group names (Nees 1812, Leach 1815, Haliday

1833b). The remaining two, Hybrizonites (containing *Hybrizon* F., *Ephedrus* Haliday, and *Praon* Haliday) and Opiites (containing 17 genera), are the oldest valid and available names for their respective family-group taxa. The subfamily name Opiinae thus dates from Blanchard (1845). Blanchard clearly states that he followed the classification of earlier authors fairly closely, but his hierarchical arrangement and use of names based on included genera makes it easier to recognize these unequivocally as family-group taxa. Paxylommatinae is currently treated as a subfamily within Ichneumonidae, and as a senior synonym of Hybrizontinae. Previously (Shenefelt 1969, Mason 1981b) the oldest family-group name for this taxon was thought to be Pachylommatoidea Foerster, 1862.

Throughout the 19th century, the family-group name based on *Sigalphus* Latreille was largely used in a very different sense than it is today. Blanchard (1845) presented a clear picture of the earliest use of the name for a group of genera containing *Sigalphus*, *Chelonus* Jurine, and *Triaspis* Haliday. When used in this sense, Sigalphinae is thus a senior synonym of Cheloninae. After Foerster's (1862) description of the Chelonoidae, and his separation of Chelonoidae from Sigalphoidae, however, the subfamily name Sigalphinae was generally misapplied to a group of helconines now known as the Brachistini. It was not until Viereck (1914) finally tied the name *Sigalphus* to its correct type species that the subfamily name took on its present meaning (Baker 1926).

Most of the better-known subfamily and tribal names in use today date from the work of Foerster (1862), who proposed a large number of family-group names for the Braconidae. Foerster proposed the following as new: Chelonoidae and Microgasteroidae (validating the species group names used by Nees), Blacoidae, Brachistoidae, Dacnusoidea, Diospiloidae, Doryctoidae, Eumicrodoidae, Euphoroidae, Euspathioidae, Exothecoidae, Hecaboloidae,

Helconoidae, Hormioidae, Ichneutoidae, Liophronoidae, Macrocentroidae, Perilitoidae, Rhyssaloidae, and Rogadoidae. Of these names, Liophronini is currently treated as a synonym of Euphorini within the Euphorinae (based on the classification of Shaw (1985)), Euspathioidae is based on an unjustified emendation (*Euspathius* Foerster, 1862) of *Spathius* Nees, 1819 within the Doryctinae, and Eumicrodoidae may also be based on an unjustified emendation, though unlike *Euspathius*, Foerster did not explicitly propose *Eumicrodus* Foerster, 1862 as an emendation for *Microdus* Nees, 1814 (only implying as much by his selection of the same type species). Eumicrodini could therefore also be interpreted as an unused senior synonym of Microdini (as the latter is defined by Sharkey (1992)) within the Agathidiinae. With the exception of these three (Liophronoidae, Eumicrodoidae, Euspathioidae), all other family-group names proposed by Foerster (1862) are currently in use as either tribes or subfamilies within the Braconidae. In those cases where several of these taxa are combined as tribes under a single subfamily, the priority of the subfamily name has been established solely on the basis of historical usage (essentially following a first reviser principle). Thus, Diospilini is treated as a tribe of Helconinae and not vice versa. The same is true for the tribal classification of the Doryctinae and Euphorinae. Only in the case of the names Hormiinae and Exothecinae has lack of consistent usage as well as uncertainties regarding relationships led to problems of priority, as explained by Wharton (1993).

Marshall (1872) was the first to use the correct form for Foerster's Euspathioidae when he proposed the family-group name Spathiides. Based on Article 35.4 (ICZN 1999), the valid family-group name must be based on the name *Spathius*, and should be attributed to Foerster (1862) despite the priority of usage of the correct form of the name by Marshall (1872). Marshall (1872)

is often overlooked as a source for newly proposed family-group names, with most authors incorrectly referring to his later publications, or sometimes to Parfitt (1881) for the family-group names Spathiides and/or Calyptides. Similarly, the family-group name Pambolides was first published by Marshall (1885), though Marshall (1887) or Marshall in Cresson (1887) is sometimes cited. Calyptinae (-ini) and Pambolinae (-ini) thus date from Marshall (1872) and Marshall (1885) respectively. As explained in detail by Mason (1974), the names Brachistinae and Brachistini have priority over Calyptinae and Calyptini even though the latter were widely used prior to Mason's (1974) publication. The spellings *Rhogas* and *Rhogadinae*, which are unjustified emendations, date from Marshall (1872).

In 1887 both Cresson (as Meteorinae) and Marshall (as Meteorides) used a family-group name based on the generic name *Meteorus* Haliday. In the report dated 26 May 1887 (Transactions of the American Entomological Society 1887: v), Cresson's paper is listed as an addition to the Society's library. Marshall's contribution is published in the June issue of the Transactions of the Entomological Society of London, and thus was published after Cresson's. Meteorinae (-ini) therefore dates from Cresson (1887), even though Cresson (1887) cites Marshall for kindly sending him a preprint of his manuscript on the British fauna. The family group name Toxoneurinae also dates from Cresson, 1887. This name was replaced with Cardiochilinae by Ashmead (1900a, 1900b) when Ashmead sank *Toxoneuron* Say, 1836 as a junior subjective synonym of *Cardiochiles* Nees, 1819. Though Toxoneurinae has priority, Cardiochilinae has gained widespread acceptance (ICZN 1999, Article 40.2), and should thus be used as the valid name for this taxon even though *Toxoneuron* has recently been reinstated (Whitfield and Dangerfield 1997).

William H. Ashmead is responsible for

several family-group names, all published in 1900. Slight confusion has arisen, however, because many of the names proposed by Ashmead were transmitted to several workers in applied entomology prior to the appearance of Ashmead's (1900b) Classification of the Ichneumonidea, and a few of the family-group names thus first became available in these other works. Despite the complexities of this matter, the names Aphrastobraconinae (-ini), Cardiochilinae (-ini), Eueurobraconinae (-ini), Orgilinae (-ini), Trioxinae (-ini), and Zelinae (-ini) should all be attributed to Ashmead, with Cardiochilinae and Orgilinae in Ashmead (1900a) and the rest in Ashmead (1900b). Ashmead (1900a, 1900b) also appears to have been the first to use Microdini in place of Foerster's Eumicrodoidae, though no specific reason was offered. As with Spathiinae, however, the family-group name Microdini should probably be attributed to Foerster (1862), since *Eumicrodus* appears to be an unjustified emendation of *Microdus* (ICZN 1999, Article 35.4). Fourteen other authors each proposed a single family-group name during the first half of the 20th century. Only Szépligeti, Viereck, Enderlein and Fahringer proposed more than one during this period. The publications by Marshall (1885, 1887, 1888, 1889, 1891), Marshall in Dalla Torre (1898), Ashmead (1900b), and Szépligeti (1904) did much to promote the use of a standard set of subfamily names in Braconidae during the 20th century, even though these names were still frequently placed within the framework of Wesmael's older groupings.

The works of Viereck (1914, 1918, 1919, 1921) are especially noteworthy as they provide explicit designations for the type species of genera and thus a clear meaning for the family-group names based on these genera. Subsequent authors have disagreed with several of Viereck's interpretations, but the value of Viereck's work lies in his attempt to provide stability for ichneumonoid classification through a rig-

orous application of the type species concept (following adoption of a set of rules for zoological nomenclature in 1901 (Règles 1905)). Gahan's (1917) use of the subfamily name *Vipiinae* and Viereck's (1918) subsequent adoption of *Vipionidae* for nine subfamilies formerly included in the *Braconidae* were a direct result of Viereck's (1914) interpretation of the type species of the genus *Bracon*. This particular interpretation led to a transfer of the name *Bracon* to the group known then and now as the *Agathidinae*. Viereck (1914) also corrected previous designations for the type species of *Sigalphus* Latreille, and further noted the possibility that *Incubus* Schrank was a senior synonym of *Aphidius* Nees. These and other actions resulted in several major changes in generic concepts and the consequent proposal of several new family-group names as replacements for existing ones no longer deemed appropriate (e.g., Bridwell 1920, Essig 1942). To counter this, various petitions (e.g., for *Bracon*) were made to the International Commission of Zoological Nomenclature to fix certain generic concepts, leading to re-establishment of the older names used by Marshall in Dalla Torre (1898), Ashmead (1900b), and Szépligeti (1904).

From the standpoint of newly proposed family-group names, the last major author of the first half of the 20th century was Fahringer. Fahringer (1928, 1929, 1930, 1936) proposed numerous new names for suprageneric taxa, principally in his monumental work, *Opuscula Braconologica*, published in several fascicles over a 12 year period. Most of the tribal and subtribal names he proposed were properly formed and thus available, but a few of them (such as the subtribe *Longiradialii*) are not because they are not based on generic names. Fahringer also provided what appear to be valid family-group names for two sections (a suprageneric category he used below subtribe).

Aside from Mackauer's (1961) proposal of seven new family-group names for

aphidiines, there were relatively few new suprageneric taxa described from 1940–1969. By contrast, there were as many new family-group names proposed from 1970–1998 as there were from 1812–1969. About 50 of the names proposed after 1969 were based on newly described genera, with nearly all of these representing new discoveries of unusual taxa rather than mere splitting of existing genera. Most of the remaining family-group taxa described after 1969 represent attempts to add structure to larger subfamilies such as the *Agathidinae*, *Doryctinae*, *Euphorinae*, and *Opiinae*. Major works containing new family-group names during this period include those of Fischer (1970, 1981a), van Achterberg (1979c, 1984a, 1988, 1995), Mason (1981a), Shaw (1985), Tobias (1987), Zettel (1990), Belokobylskij (1992, 1993), and Sharkey (1992).

A few of the family-group names first proposed after 1930 apparently do not meet the criteria for availability set out in Article 13 of the previous edition of the Code (ICZN 1985). Under this provision, names proposed in catalogues, if such names were unaccompanied by descriptions, are unavailable (e.g., *Cosmophorinae* Muesebeck and Walkley, 1951). However, a new provision, Article 13.2.1 (ICZN 1999), provides an exception for names (such as *Cosmophorinae*) proposed between 1930 and 1961. Article 13 may also apply to names first proposed in discussions of relationships among higher taxa, when there is no clear statement on how the newly named taxon is differentiated (e.g., Čapek 1965). In such cases, it is also difficult to determine when these names first meet the criteria of availability. We have noted these problems in brackets in the chronological list below, as well as our proposals for when the names first became available. Our findings are summarized below in two forms: a chronological list of all family-group names known to us and an appendix of all proposed names in alphabetical order.

CHRONOLOGICAL LIST OF FAMILY-
GROUP NAMES IN BRACONIDAE,
USING SPELLINGS AS ORIGINALLY
PROPOSED

The list below contains all family-group names known to us with the exception of those not based on generic names. Names are followed by their author, date first proposed, and page number where the name is first found. Complete citations for each author are in the Literature Cited. We are aware that there are many variant spellings that have been used subsequent to the first proposal of these names (especially before standardization of endings for family-group names), but we have not treated them here. We have focused our attention on the priority of names, and have thus also avoided discussion of the important issue of correct spellings for the most part. Where useful, we include additional information on validity and availability in brackets, especially for younger names thought to have had priority.

Bracones Nees, 1812: 3.

Bassi Nees, 1812: 3 [invalid name; based on junior homonym (*Bassus* Nees, 1814, not *Bassus* Fabricius, 1804)].

Alysiada Leach, 1815: 143 [= Alysiidae Stephens, 1929: 355].

Cheloni Nees, 1816: 260 [unavailable name, see introduction].

Aphidini Haliday, 1833b: 482.

Sigalphini Haliday, 1833b: 482 [= Sigalphites Blanchard, 1845: 157].

Agathenes Haliday, 1833b: 482 [= Agathites Blanchard, 1845: 157].

Opiites Blanchard, 1845: 157.

Euspathioidae Foerster, 1862: 227.

Hecaboloidae Foerster, 1862: 227.

Doryctoidae Foerster, 1862: 227.

Hormioidae Foerster, 1862: 227.

Rogadoidae Foerster, 1862: 228.

Rhyssaloidae Foerster, 1862: 228.

Chelonoidae Foerster, 1862: 228.

Microgasteroidae Foerster, 1862: 228.

Eumicrodoidae Foerster, 1862: 228.

Euphoroidae Foerster, 1862: 228.

Perilitoidae Foerster, 1862: 228.

Brachistoidae Foerster, 1862: 229.

Blacoidae Foerster, 1862: 229.

Liophronoidae Foerster, 1862: 229.

Ichneutoidae Foerster, 1862: 229.

Helconoidae Foerster, 1862: 229.

Macrocentroidae Foerster, 1862: 229.

Diospiloidae Foerster, 1862: 229.

Dacnusoidea Foerster, 1862: 229.

Exothecoidae Foerster, 1862: 279.

Spathiides Marshall, 1872: 97.

Rhogadides Marshall, 1872: 99.

Calyptides Marshall, 1872: 116.

Pambolides Marshall, 1885: 9.

Meteorinae Cresson, 1887: 55.

Toxoneurinae Cresson, 1887: 55.

Orgilini Ashmead, 1900a: 590.

Cardiochilinae Ashmead, 1900a: 592.

Microdini Ashmead, 1900a: 592.

Alloeini Ashmead, 1900b: 104.

Aphrastobraconini Ashmead, 1900b: 136.

Euurobraconini Ashmead, 1900b: 136.

Trioxini Ashmead, 1900b: 113.

Zelini Ashmead, 1900b: 118.

Cenocoelionidae Szépligeti, 1901: 353.

Gnathobraconinae Szépligeti, 1904a: 2.

Mimagathidinae Enderlein, 1905: 449.

Holcobraconini Cameron, 1905: 90.

Leiophroninae Schmiedeknecht, 1907: 511 [first correct spelling of Liophronoidae Foerster, 1862].

Helorimorphinae Schmiedeknecht, 1907: 511.

Microtypinae Szépligeti, 1908: 426.

Capitoniidae Viereck, 1910: 616.

Trachypetinae Schulz, 1911: 85.

Stephaniscinae Enderlein, 1912: 1 [invalid name, based on junior homonym].

Psenobolini Enderlein, 1912: 2 [= Psenobolina Belokobylskij, 1992: 922].

Pseudospathiini Enderlein, 1912: 2.

Vipiinae Gahan, 1917: 196 [= Vipioninae Viereck, 1918: 69].

Elasmosominae Viereck, 1918: 69.

Mesocoelinae Viereck, 1918: 69.

Apantelinae Viereck, 1918: 69.

Miracinae Viereck, 1918: 69.

Adelinae Viereck, 1918: 69 [= Acoeliini Telenga, 1955: 14].

- Bassinae Viereck, 1918: 70.
 Triaspininae Viereck, 1918: 71.
 Pelecystominae Viereck, 1918: 71.
 Neoneurinae Bengtsson, 1918: 27.
 Coeliniinae Viereck, 1919a: 48.
 Stantoninae Viereck, 1919b: 198.
 Microbraconinae Bridwell, 1920: 389.
 Ypsistocerinae Cushman, 1923: 54.
 Phanerotomini Baker, 1926: 453.
 Aleiodinae Muesebeck, 1928: 901.
 Atanycoloidea Fahringer, 1928: 7 [proposed as a Sectio].
 Iphiaulacoidea Fahringer, 1928: 7.
 Habrobraconini Fahringer, 1928: 7.
 Gastrothecini Fahringer, 1928: 7 [incorrectly attributed to Foerster; invalid name, based on junior homonym].
 Phanomerini Fahringer, 1928: 7.
 Acanthobraconini Fahringer, 1928: 7.
 Rhaconotini Fahringer, 1928: 8.
 Pseudostephaniscini Fahringer, 1928: 8 [unavailable, not based on a valid generic name].
 Baeocentrini Fahringer, 1928: 8.
 Rhamnurini Fahringer, 1929: 234 [= Rhamnurini van Achterberg, 1981: 88].
 Histeromerini Fahringer, 1930: 121.
 Gynocryptinae Quilis Pérez, 1931: 26.
 Incubinae Brues and Melander, 1932: 482 [published as junior synonym of Aphidiinae].
 Chiviniini Shestakov, 1932: 258.
 Pseudodicrogeniinae Fahringer, 1936: 572.
 Aneurobraconinae Fahringer, 1936: 587.
 Incubidae Essig, 1942: 644 [first valid treatment of name, which then becomes available as of 1932 (ICZN 1999, Article 11.6.1)].
 Minangina De Saeger, 1948: 71.
 Odontobraconinae Granger, 1949: 17.
 Cosmophorinae Muesebeck and Walkley, 1951: 183 [*nomen nudum* but possibly valid under Article 13.2.1].
 Neobraconinae Hellén, 1957: 33 [*nomen nudum*; attributed to Fahringer, thus probably a misspelling of Neorhacodinae].
 Chremylini Hellén, 1957: 34.
 Acrisidini Hellén, 1957: 35.
 Ecphylini Hellén, 1957: 36.
 Coeloidini Tobias, 1957: 1347.
 Glyptomorphini Tobias, 1957: 1348.
 Cosmophorinae Čapek, 1958: 153 [the first publication in which this name satisfies criterion of availability under Article 13.1].
 Iseurini Hedqvist, 1959: 486 [incorrectly included in Megalyridae].
 Ephedrinae Mackauer, 1961: 794.
 Prainae Mackauer, 1961: 794.
 Aclitinae Mackauer, 1961: 795.
 Paralipsina Mackauer, 1961: 800.
 Lysiphlebina Mackauer, 1961: 800.
 Protaphidiina Mackauer, 1961: 801.
 Monoctonina Mackauer, 1961: 801.
 Telengainae Tobias, 1962: 269.
 Centistinae Čapek, 1965: 99 [*nomen nudum*, available from Čapek 1970].
 Meteorideinae Čapek, 1965: 99. [apparent *nomen nudum*; if so, available from Tobias 1967].
 Meteorideinae Tobias, 1967: 395.
 Lysitermini Tobias, 1968: 28.
 Archaphidina Mackauer, 1968: 30.
 Muesebeckiini Mason, 1969: 263.
 Centistinae Čapek, 1970: 867.
 Ademonini Fischer, 1970: 82.
 Gnaptodonina Fischer, 1970: 85 [= Gnaptodontinae Fischer 1970 as a result of ICZN Opinion 1424 (1987)].
 Biosterina Fischer, 1970: 85.
 Coleopiina Fischer, 1970: 85.
 Pokomandyina Fischer, 1970: 86.
 Desmiostomini Fischer, 1972: 55 [= Desmiostomatini Fischer, 1972: 56].
 Mesostoinae van Achterberg, 1975: 158.
 Proteropini van Achterberg, 1976: 43.
 Zemiotini van Achterberg, 1976: 44.
 Gnaptogastrini Tobias, 1976b: 319.
 Exodontiellini Wharton, 1978: 298.
 Apozygidae Mason, 1978: 609.
 Betylobraconinae Tobias, 1979: 130.
 Cercobarconinae Tobias, 1979: 134.
 Amicrocentrinae van Achterberg, 1979a: 1.
 Xiphozelinae van Achterberg, 1979b: 29.
 Charmontini van Achterberg, 1979c: 241.
 Homolobinae van Achterberg, 1979c: 241.
 Microplitini Mason, 1981a: 24.

- Forniciini Mason, 1981a: 24.
 Cotesiini Mason, 1981a: 24.
 Evaniodini Fischer, 1981a: 44.
 Binareina Fischer, 1981a: 45.
 Dendrosotina Fischer, 1981a: 45.
 Stenocorsina Fischer, 1981a: 45.
 Heterospilini Fischer, 1981a: 45.
 Neoclinocentrina Fischer, 1981a: 45.
 Pedinotina Fischer, 1981a: 46.
 Bitomina Fischer, 1981b: 29.
 Mononeurina Fischer, 1981c: 47.
 Khoikhoiinae Mason, 1983: 49.
 Brulleiini van Achterberg, 1983a: 281.
 Adeshini van Achterberg, 1983b: 175.
 Dirrhopinae van Achterberg, 1984a: 41.
 Acampsini van Achterberg, 1984a: 41 [apparent *nomen nudum*].
 Dyscoletini van Achterberg, 1984a: 41 [apparent *nomen nudum*].
 Leptorhaconotini van Achterberg, 1984a: 41 [apparent *nomen nudum*].
 Aspidobraconina van Achterberg, 1984b: 137.
 Physaraiina van Achterberg, 1984b: 137.
 Rhysipolini Belokobylskij, 1984: 1021.
 Dinocampini Shaw, 1985: 277.
 Townesilitini Shaw, 1985: 277.
 Microctonini Shaw, 1985: 277.
 Loxocephalini Shaw, 1985: 277 [apparent *nomen nudum*; also invalid based on junior homonym].
 Syntretini Shaw, 1985: 277.
 Ecnomiinae van Achterberg, 1985: 341.
 Pselaphanini van Achterberg, 1985: 341.
 Victoroviellini Tobias, 1986: 95.
 Cryptoxilonini Tobias, 1986: 183.
 Diospilittinae Tobias, 1987: 845.
 Acampsohelconini Tobias, 1987: 847.
 Chelonohelconini Tobias, 1987: 847.
 Oncometeorini Tobias, 1987: 848.
 Prosyntretini Tobias, 1987: 850.
 Semionini Tobias, 1987: 854.
 Vaepellinae Quicke, 1987a: 73.
 Bathyaulacini Quicke, 1987b: 43.
 Antestrigini van Achterberg, 1987: 3.
 Praonopterinae Tobias, 1988: 645.
 Lissogastrini Oltra and Michelena, 1988: 165.
 Chalaropini van Achterberg, 1988: 3.
 Blacozonini van Achterberg, 1988: 3.
 Stegnozellini van Achterberg, 1988: 3.
 Dyscoletini van Achterberg, 1988: 3 [apparently the first publication in which this name satisfies criterion of availability under Article 13].
 Isomecini Tobias, 1990: 174.
 Pentatermini Belokobylskij, 1990: 116.
 Odontosphaeropygini Zettel, 1990: 147.
 Phanerotomellina Zettel, 1990: 147.
 Pseudophanerotomini Zettel, 1990: 147.
 Pseudohelconina van Achterberg, 1990a: 283.
 Pronkiini van Achterberg, 1990b: 169.
 Yeliconini van Achterberg, 1991a: 3.
 Clinocentrini van Achterberg, 1991a: 3.
 Argamaniini van Achterberg, 1991b: 204.
 Afrocampsiini van Achterberg and Austin, 1992: 3.
 Acampsini van Achterberg and Austin, 1992: 3 [apparently the first publication in which this name satisfies criterion of availability under Article 13].
 Doryctomorphina Belokobylskij, 1992: 908.
 Caenophanina Belokobylskij, 1992: 908.
 Acanthodoryctina Belokobylskij, 1992: 910.
 Ivondroviina Belokobylskij, 1992: 912.
 Pambolideina Belokobylskij, 1992: 913.
 Percnobraconoidina Belokobylskij, 1992: 915.
 Labaniini Belokobylskij, 1992: 917.
 Sericobraconini Belokobylskij, 1992: 918.
 Spathiostenina Belokobylskij, 1992: 920.
 Leptorhaconotini Belokobylskij, 1992: 920 [apparently the first publication in which this name satisfies criterion of availability under Article 13].
 Sisupalina Belokobylskij, 1992: 921.
 Trigonophasmina Belokobylskij, 1992: 921.
 Ptesimogastrina Belokobylskij, 1992: 922.
 Spathioplittina Belokobylskij, 1992: 922.
 Percnobraconini Belokobylskij, 1992: 924.
 Westwoodiellini van Achterberg, 1992: 359.
 Cremnoptini Sharkey, 1992: 425.
 Disophrini Sharkey, 1992: 425.
 Earinini Sharkey, 1992: 425.

Hydrangeocolini Whitfield, 1992: 274 [possibly a *nomen nudum*].
 Dimerina Belokobylskij, 1993: 145.
 Oncophanina Belokobylskij, 1993: 148.
 Acanthormiina Belokobylskij, 1993: 151.
 Tritermina Belokobylskij, 1993: 152.
 Cedriina Belokobylskij, 1993: 154.
 Chremylomorphini Belokobylskij, 1993: 155.
 Canberriini Belokobylskij, 1993: 156.
 Monitoriellini Belokobylskij, 1993: 156.
 Avgini Belokobylskij, 1993: 157.
 Leuriniina Belokobylskij, 1993: 158.
 Parahormiina Belokobylskij, 1993: 158.
 Austrohormiini Belokobylskij, 1993: 159.
 Stiropiini van Achterberg, 1993: 25.
 Syngastrini van Achterberg, 1993: 55 [*nomen nudum*].
 Ussurohelconini van Achterberg, 1994: 3.
 Siragrini Belokobylskij, 1994: 141.
 Maxfischeriini Papp, 1994: 143.
 Mendesellinae Whitfield and Mason, 1994: 61.
 Facitorini van Achterberg, 1995: 3.
 Mannokeraiiini van Achterberg, 1995: 3.
 Masoninae (-ini) van Achterberg, 1995: 3.
 Planitorini van Achterberg, 1995: 3.
 Embobraconina van Achterberg, 1995: 4.
 Tetratermini van Achterberg, 1996: 249.
 Xyeloblacini van Achterberg and Altenhofer, 1997: 291.
 Myiocephalini Chen and van Achterberg, 1997: 3.
 Vervoortihelconina van Achterberg, 1998: 401.
 Excluded names (not Braconidae):
 Hybrizonites Blanchard, 1845: 155 [belongs to Ichneumonidae, as senior synonym of Paxylommatinae Foerster].
 Excultinae Sharma, 1984. Reichenbachia 22: 76 [belongs to Chrysididae].

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APPENDIX 1

The following is an alphabetical list of family-group names in the Braconidae, with indication of their subfamily placement. Though classifications vary from author to author, and are presently controversial, the subfamily arrangement used here is based largely on Quicke and van Achterberg (1990) and van Achterberg (1993, 1995). Tribes and subtribes largely follow Mackauer (1968), Mason (1981), van Achterberg (1987, 1988, 1991b, 1992, 1994, 1995), Shaw (1985), Quicke (1987), Zettel (1990), Belokobylskij (1992), Sharkey (1992), and van Achterberg and Austin (1992).

Acampsiini van Achterberg and Austin, 1992 (Sigalphinae)

Acampsohelconini Tobias, 1987 (Cenocoeliinae)

Acanthobraconini Fahringer, 1928 (Braconinae)

Acanthodoryctina Belokobylskij, 1992 (Doryctinae)

- Acanthohormiini Belokobylskij, 1993 (Lysiterminae)
 Acitina Mackauer, 1961 (Aphidiinae)
 Acrisidini Hellén, 1957 (Rhyssalinae)
 Adeliinae Viereck, 1918 (Adeliinae)
 Ademonini Fischer, 1970 (Opiinae)
 Adeshini van Achterberg, 1983 (Braconinae)
 Afrocampisini van Achterberg and Austin, 1992 (Sigalphinae)
 Agathidinae (-ini) Haliday, 1833 (Agathidinae)
 Aleiodini Muesebeck, 1928 (Rogadinae)
 Alloeini Ashmead, 1900 (Alysiinae)
 Alysiinae (-ini) Leach, 1815 (Alysiinae)
 Amicrocentrinae van Achterberg, 1979 (Amicrocentrinae)
 Aneurobraconini Fahringer, 1936 (Agathidinae)
 Antestrigini van Achterberg, 1987 (Orgilinae)
 Apantelini Viereck, 1918 (Microgastrinae)
 Aphidiinae (-ini) Haliday, 1833 (Aphidiinae)
 Aphrastobraconini Ashmead, 1900 (Braconinae)
 Apozyginae Mason, 1978 (Apozyginae)
 Archaphidina Mackauer, 1968 (Aphidiinae)
 Argamaniini van Achterberg, 1991 (Braconinae)
 Aspidobraconina van Achterberg, 1984 (Braconinae)
 Atanycolina Fahringer, 1928 (Braconinae)
 Austrohormiini Belokobylskij, 1993 (Hormiinae)
 Avgini Belokobylskij, 1993 (Hormiinae)
 Baecentrini Fahringer, 1928 (Opiinae)
 Bassinae Nees, 1812 (invalid)
 Bassinae Viereck, 1918 (Agathidinae)
 Bathyaulacini Quicke, 1987 (Braconinae)
 Betylobraconinae (-ini) Tobias, 1979 (Betylobraconinae)
 Binareini Fischer, 1981 (Doryctinae)
 Biosterini Fischer, 1970 (Opiinae)
 Bitomina Fischer, 1981 (Opiinae)
 Blacinae (-ini) Foerster, 1862 (Blacinae)
 Blacozonini van Achterberg, 1988 (Blacinae)
 Brachistini Foerster, 1862 (Helconinae)
 Braconidae (-inae) Nees, 1812
 Brulleiini van Achterberg, 1983 (Helconinae)
 Caenophanina Belokobylskij, 1992 (Doryctinae)
 Calyptini Marshall, 1872 (Helconinae)
 Canberriini Belokobylskij, 1993 (Hormiinae)
 Capitoniini Viereck, 1910 (Cenocoeliinae)
 Cardiochilinae Ashmead, 1900 (1887) (Cardiochilinae)
 Cedriina Belokobylskij, 1993 (Pambolinae)
 Cenocoeliinae (-ini) Szépligeti, 1901 (Cenocoeliinae)
 Centistini Čapek, 1970 (Euphorinae)
 Cercobarconini Tobias, 1979 (Trachypetinae)
 Chalaropini van Achterberg, 1988 (Blacinae)
 Charmontinae van Achterberg, 1979 (Charmontinae)
 Cheloninae (-ini) Foerster, 1862 (Cheloninae)
 Chelonohelconini Tobias, 1987 (Helconinae)
 Chiviniini Shestakov, 1932 (Braconinae)
 Chremylini Hellén, 1957 (Pambolinae)
 Chremylomorphina Belokobylskij, 1993 (Pambolinae)
 Clinocentrini van Achterberg, 1991 (Rogadinae)
 Coeliina Viereck, 1919 (Alysiinae)
 Coeloidini Tobias, 1957 (Braconinae)
 Coleopiina Fischer, 1970 (Opiinae)
 Cosmophorini Čapek, 1958 (Euphorinae)
 Cotesiini Mason, 1981 (Microgastrinae)
 Cremnoptini Sharkey, 1992 (Agathidinae)
 Cryptoxilonini Tobias, 1986 (Euphorinae)
 Dacnusiini Foerster, 1862 (Alysiinae)
 Dendrosotina Fischer, 1981 (Doryctinae)
 Desmlostomatini Fischer, 1972 (Opiinae)
 Dimerina Belokobylskij, 1993 (Pambolinae)
 Dinocampini Shaw, 1985 (Euphorinae)
 Diospilinae Tobias, 1987 (Aphidiinae)
 Diospilini Foerster, 1862 (Helconinae)
 Dirrhopinae van Achterberg, 1984 (Dirrhopinae)
 Disophrini Sharkey, 1992 (Agathidinae)
 Doryctinae (-ini) Foerster, 1862 (Doryctinae)
 Doryctomorphina Belokobylskij, 1992 (Rhyssalinae)
 Dyscoletini van Achterberg, 1988 (Blacinae)
 Eariniini Sharkey, 1992 (Agathidinae)
 Ecnomiinae van Achterberg, 1985 (Ecnomiinae)
 Ecphylini Hellén, 1957 (Doryctinae)
 Elasmosomini Viereck, 1918 (Neoneurinae)
 Embobraconina van Achterberg, 1995 (Doryctinae)
 Ephedrini Mackauer, 1961 (Aphidiinae)
 Euphorinae (-ini) Foerster, 1862 (Euphorinae)
 Euurobraconini Ashmead, 1900 (Braconinae)
 Evaniiodini Fischer, 1981 (Doryctinae)
 Excultinae Sharma, 1984 (Chrysididae)
 Exodontiellini Wharton, 1978 (Opiinae)
 Exothecinae Foerster, 1862 (Exothecinae)
 Facitorini van Achterberg, 1995 (Betylobraconinae)
 Forniciini Mason, 1981 (Microgastrinae)
 Gastrothecini Fahringer, 1928 (invalid)
 Glyptomorphina Tobias, 1957 (Braconinae)
 Gnaptodontinae Fischer, 1970 (Gnaptodontinae)
 Gnaptogastrini Tobias, 1976 (Gnaptodontinae)
 Gnathobraconini Szépligeti, 1904 (Braconinae)
 Gynocryptina Quilis Perez, 1931 (Aphidiinae)
 Habrobraconini Fahringer, 1928 (Braconinae)
 Hecabolini Foerster, 1862 (Doryctinae)
 Helconinae (-ini) Foerster, 1862 (Helconinae)
 Helorimorphini Schmiedeknecht, 1907 (Euphorinae)
 Heterospilini Fischer, 1981 (Doryctinae)
 Histeromerinae Fahringer, 1930 (Histeromerinae)
 Holcobraconini Cameron, 1905 (Doryctinae)
 Homolobinae (-ini) van Achterberg, 1979 (Homolobinae)
 Hormiinae (-ini) Foerster, 1862 (Hormiinae)
 Hydrangeocolini Whitfield, 1992 (Hormiinae)
 Ichneutinae (-ini) Foerster, 1862 (Ichneutinae)
 Incubinae Brues and Melander, 1932 (Aphidiinae)
 Iphiaulacini Fahringer, 1928 (Braconinae)
 Isomecina Tobias, 1990 (Braconinae)
 Iseurini Hedqvist, 1959 (Cenocoeliinae)
 Ivondroviina Belokobylskij, 1992 (Doryctinae)
 Khoikhoiinae Mason, 1983 (Khoikhoiinae)
 Labaniini Belokobylskij, 1992 (Doryctinae)
 Leiophronini Foerster, 1862 (Euphorinae)

- Leptorhaconotini Belokobylskij, 1992 (Doryctinae)
 Leuriniini Belokobylskij, 1993 (Hormiinae)
 Lissogastrini Oltra and Michelena, 1988 (Microgastrinae)
 Loxocephalini Shaw, 1985 (invalid)
 Lysiphlebinina Mackauer, 1961 (Aphidiinae)
 Lysiterminae (-ini) Tobias, 1968 (Lysiterminae)
 Macrocentrinae Foerster, 1862 (Macrocentrinae)
 Mannokeraiini van Achterberg, 1995 (Masoninae)
 Masoninae (-ini) van Achterberg, 1995 (Masoninae)
 Maxfischeriini Papp, 1994 (Helconinae)
 Mendesellinae Whitfield and Mason, 1994 (Mendesellinae)
 Mesocoelini Viereck, 1918 (Agathidinae)
 Mesostoinae van Achterberg, 1975 (Mesostoinae)
 Meteorideinae (-ini) Čapek, 1965 (Meteorideinae)
 Meteorini Cresson, 1887 (Euphorinae)
 Microbraconini Bridwell, 1920 (Braconinae)
 Microctonini Shaw, 1985 (Euphorinae)
 Microdini Foerster, 1862 (Agathidinae)
 Microgastrinae (-ini) Foerster, 1862 (Microgastrinae)
 Microplitini Mason, 1981 (Microgastrinae)
 Microtypinae Szépligeti, 1908 (Microtypinae)
 Mimagathidini Enderlein, 1905 (Orgilinae)
 Minangini De Saeger, 1948 (Sigalphinae)
 Miracinae Viereck, 1918 (Miracinae)
 Monitoriellini Belokobylskij, 1992 (Rhyssalinae)
 Monotonina Mackauer, 1961 (Aphidiinae)
 Mononeurina Fischer, 1981 (Doryctinae)
 Muesebeckiini Mason, 1969 (Ichneutinae)
 Myiocephalini Chen and van Achterberg, 1997 (Euphorinae)
 Neobraconinae Hellén, 1957 (nomen nudum)
 Neoclinocentrina Fischer, 1981 (Doryctinae)
 Neoneurinae (-ini) Bengtsson, 1918 (Neoneurinae)
 Odontobraconina Granger, 1949 (Doryctinae)
 Odontosphaeropygini Zettel, 1990 (Cheloninae)
 Oncometeorini Tobias, 1987 (Euphorinae)
 Oncophanina Belokobylskij, 1993 (Rhyssalinae)
 Opiinae (-ini) Blanchard, 1845 (Opiinae)
 Orgilinae (-ini) Ashmead, 1900 (Orgilinae)
 Pambolideina Belokobylskij, 1992 (Doryctinae)
 Pambolinae (-ini) Marshall, 1885 (Pambolinae)
 Parahormiini Belokobylskij, 1993 (Hormiinae)
 Paralipsina Mackauer, 1961 (Aphidiinae)
 Pedinotina Fischer, 1981 (Doryctinae)
 Pelecystomini Viereck, 1918 (Rogadinae)
 Pentatermini Belokobylskij, 1990 (Lysiterminae)
 Percnobraconini Belokobylskij, 1992 (Doryctinae)
 Percnobraconoidina Belokobylskij, 1992 (Doryctinae)
 Perilitini Foerster, 1862 (Euphorinae)
 Phanerotomellina Zettel, 1990 (Cheloninae)
 Phanerotomini Baker, 1926 (Cheloninae)
 Phanomerini Fahringer, 1928 (Exothecinae)
 Physaraiini van Achterberg, 1984 (Braconinae)
 Planitorini van Achterberg, 1995 (Betylobraconinae)
 Pokomandyina Fischer, 1970 (Opiinae)
 Praini Mackauer, 1961 (Aphidiinae)
 Praonopterinae Tobias, 1988 (Mesostoinae)
 Pronkiini van Achterberg, 1990 (Meteorideinae)
 Prosyntretina Tobias, 1987 (Euphorinae)
 Protaphidiina Mackauer, 1961 (Aphidiinae)
 Proteropini van Achterberg, 1976 (Ichneutinae)
 Pselaphaninae van Achterberg, 1985 (Pselaphaninae)
 Psenobolina Enderlein, 1912 (Doryctinae)
 Pseudodicrogeniini Fahringer, 1936 (Braconinae)
 Pseudohelconina van Achterberg, 1990 (Helconinae)
 Pseudophanerotomina Zettel, 1990 (Cheloninae)
 Pseudospathiini Enderlein, 1912 (Doryctinae)
 Pseudostephaniscini Fahringer, 1928 (Doryctinae)
 Ptesimogastrina Belokobylskij, 1992 (Doryctinae)
 Rhaconotina Fahringer, 1928 (Doryctinae)
 Rhamnurini Fahringer, 1929 (Braconinae)
 Rhysipolinae Belokobylskij, 1984 (Rhysipolinae)
 Rhyssalinae (-ini) Foerster, 1862 (Rhyssalinae)
 Rogadinae (-ini) Foerster, 1862 (Rogadinae)
 Semionini Tobias, 1987 (Microgastrinae)
 Sericobraconini Belokobylskij, 1992 (Doryctinae)
 Sigalphinae (-ini) Haliday, 1833 (Sigalphinae)
 Siragrini Belokobylskij, 1994 (Doryctinae)
 Sisupalina Belokobylskij, 1992 (Doryctinae)
 Spathiini Foerster, 1862 (Doryctinae)
 Spathioplitina Belokobylskij, 1992 (Doryctinae)
 Spathiostenina Belokobylskij, 1992 (Doryctinae)
 Stantonini Viereck, 1919 (Orgilinae)
 Stegnocellini van Achterberg, 1988 (Blacinae)
 Stenocorsina Fischer, 1981 (Doryctinae)
 Stephaniscini Enderlein, 1912 (invalid)
 Stiropiini van Achterberg, 1993 (Rogadinae)
 Syngastrini van Achterberg, 1993 (nomen nudum)
 Syntretini Shaw, 1985 (Euphorinae)
 Telengaiinae Tobias, 1962 (Telengaiinae)
 Tetratermini van Achterberg, 1996 (Lysiterminae)
 Townesilitina Shaw, 1985 (Euphorinae)
 Toxoneurinae Cresson, 1887 (invalid)
 Trachypetinae (-ini) Schulz, 1911 (Trachypetinae)
 Triaspina Viereck, 1918 (Helconinae)
 Trigonophasmina Belokobylskij, 1992 (Doryctinae)
 Trioxina Ashmead, 1900 (Aphidiinae)
 Triterminae Belokobylskij, 1993 (Lysiterminae)
 Ussurohelconini van Achterberg, 1994 (Cenocoeliinae)
 Vaepellinae Quicke, 1987 (Vaepellinae)
 Vervoortihelconina van Achterberg, 1998 (Helconinae)
 Victoroviellina Tobias, 1986 (Braconinae)
 Vipiina Gahan, 1917 (Braconinae)
 Westwoodiellini van Achterberg, 1992 (Homolobinae)
 Xiphozelinae van Achterberg, 1979 (Xiphozelinae)
 Xyeloblacini van Achterberg and Altenhofer, 1997 (Blacinae)
 Yeliconini van Achterberg, 1991 (Rogadinae)
 Ypsistocerini Cushman, 1923 (Doryctinae)
 Zelini Ashmead, 1900 (Euphorinae)
 Zemiotini van Achterberg, 1976 (Euphorinae)

Taxonomic Notes on Costa Rican Mendesellinae (Ichneumonoidea: Braconidae), with Description of a New Central American Species of *Mendesella*

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Abstract.—One new species of mendeselline braconid wasp is described, *Mendesella orianae* Valerio and Whitfield sp. nov., and the male of *Epsilogaster tico* Whitfield and Mason is described for the first time. *Mendesella orianae* from Costa Rica represents the northernmost record of *Mendesella* in the Americas, and the first recorded species of this genus in Costa Rica. The male genitalia of *E. tico* is also described, providing the first record of male genitalic characters for the subfamily Mendesellinae.

The braconid subfamily Mendesellinae was described by Whitfield & Mason (1994), who included two genera and nine species, all new. So far as is known, the species are endoparasitoids of Lepidoptera feeding within plant tissue, but biological records are sparse, and specimens of this subfamily are rarely collected in general. Since the original description there has been no further review of the distribution and biology of the known species, nor any further species described. Recently, new specimens of both genera in the subfamily have been discovered by the senior author in the collections of the Instituto Nacional de Biodiversidad (INBio). The new records add significantly to the known geographical distribution of mendeselline genera, as well as the morphology of male Mendesellinae. One of the species is new to science and it is describe below.

MATERIAL AND METHODS

The morphological terminology used in the species descriptions is that of Huber and Sharkey (1993), and Schuh (1989); except for the morphology of the propodeum, which is used *sensu* Townes (1969, Fig. E). The cuticular sculpturing terminology is that of Harris (1979), while the terminology for the wing venation is a variation of the Comstock-Needham system used by Sharkey and Wharton (1997, Fig. 15).

The metasoma of one specimen of *Epsilogaster tico* was detached, placed in warm 10% KOH overnight, and run through ethanol and xylene baths into Euparal mounting medium for slide-mounting. The male genitalia were pulled away from the remainder of the metasoma and illustrated using a microprojector.

Epsilogaster tico Whitfield and Mason
1994

(Figs. 1a, 2, 3)

Male.—Body color: Mainly light yellow; scape and pedicel light brown as face, vertex, frons, hind tarsomeres, middle telo-

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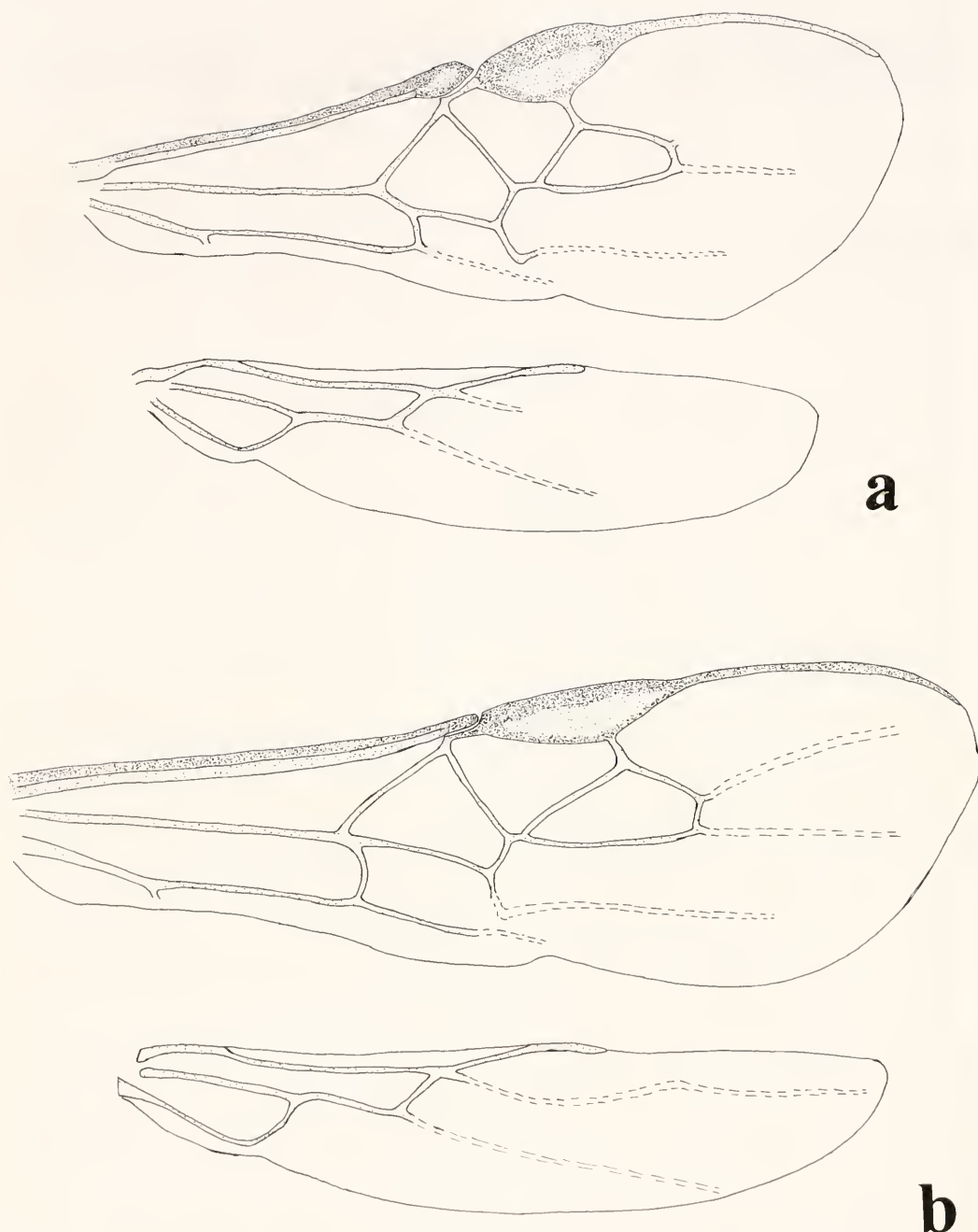
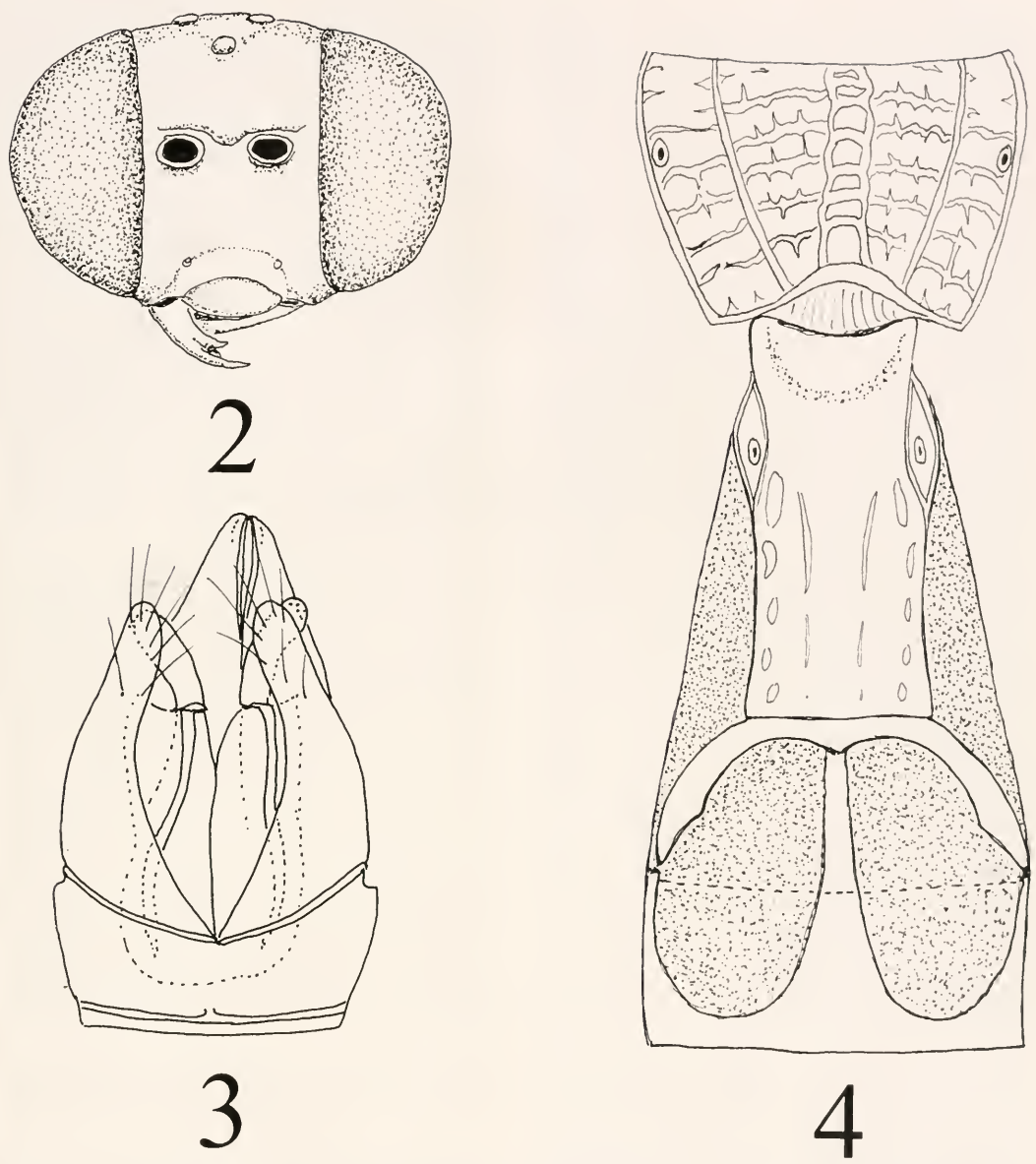


Fig. 1. Wing venation for male *Epsilogaster tico* Whitfield & Mason (a), and for female *Mendesella orianae* Valerio & Whitfield sp. nov. (b).

tarsus and metasomal terga 4–6; metanotum with darker yellow than remainder mesosoma; compound eyes silver; palpus whitish-yellow. Fore and hind wings hy-

aline (Fig. 1a); wing veins with light yellow coloration. Body length = 2.61–2.75 mm; Fore wing length = 2.44–2.47 mm. **Head:** head height/compound eye height



Figs. 2-4. 2,3. *Epsilogaster tico*, male, 2, Face, showing enlarged eyes. 3, Genital capsule. 4, Propodeum and anterior metasomal tergites of *Mendesella oriana*, sp. nov.

= 1.17-1.18; head height/compound eye length = 1.53-1.65; length of first antennal flagellomere = 0.18-0.22 mm; length of first antennal flagellomere/width of first antennal flagellomere = 4.40-5.20; length of first antennal flagellomere/length of second antennal flagellomere = 1.29-1.44; length of first antennal flagellomere/

length of third antennal flagellomere = 1.38-1.44; distal flagellomere length/width of distal flagellomere = 4.67-5.0; intertentorial pit distance = 0.13-0.16 mm; ocell-ocular distance = 0.03-0.04 mm; distance between toruli and tentorial pits = 0.25-0.27 mm; face wide at dorsal edge of clypeus = 0.28 mm. Antenna with 27 fla-

gellomeres; face nitid, without punctate sculpturing, but with few scattered obscure rugulose sculpturing features; vertex and gena with coarsely-punctate sculpturing as on posterior-ventral area of head; occiput nitid; malar suture present; malar space very short; ocelli forming an equilateral triangle. **Mesosoma:** mesosomal length/mesosomal width = 1.43–1.55, mesosomal height = 0.60–0.61 mm; hind tibia length/hind tibia maximum width = 3.60–3.89; propleural distal edge with a ridge; pronotum with mid longitudinal area with scrobiculate sculpturing; mesonotum evenly setose throughout; notaulus conspicuously foveate throughout; area at notaulus union without a depressed area and some punctate sculpturing present by setae; union of notaulus near transscutal articulation; transscutal articulation with a smooth carina that is absent laterally; scutellar sulcus wide, with 3 deep pits present; scutellum subpentagonal, without any posterior apico-medial pits or sculpturing; antero-medial area of metanotum with two subcircular pits, remainder of medial area nitid; axillary troughs of mesonotum with spaced scrobiculate sculpturing; metapleuron dorsally nitid, remainder with areolate-rugulose sculpturing present; propodeum, parallel mid-longitudinal carinae united by complete transversal carinae between them, remainder with areolate-rugulose sculpturing present, latero-longitudinal carinae cristate as mid-longitudinal carinae (no other carinae as cristate), areas between carinae nitid or with fine obscure colliculate sculpturing present. **Metasoma:** distal width of tergum 1/ basal width of tergum 1 = 0.38–0.39; length of tergum 1/ distal width of tergum 1 = 4.0–4.40; first metasomal tergum: dorso-lateral carinae with well-defined and cristate dorsal carinae curving close to one another apically and extending 0.70 length of tergum, conspicuously cristate basally; rugulose sculpturing densely present dorsally on tergum, remainder with more widely spaced rugu-

lose sculpturing, medial area raised forming two semicircular lower areas that contain 5 costulae each; terga 2–6 smooth and unsculptured, also terga 2–6 much more strongly desclerotized than first metasomal tergum.

Material examined.—Described from two males: Costa Rica, Alajuela, RNVs Caño Negro, Playuelas, 20 m. 1–18/ii/1994, Col. K. Martinez.

Comments.—The studied males have a more elongate metasoma and strongly enlarged compound eyes than the known female (Fig. 2). Also, *E. tico* male eyes are strongly enlarged in comparison with those described for *E. bicolor*, the only other males known for the genus.

The male genitalia (Fig. 3) are the first to be described for a mendeselline braconid. As with most Cardiochilinae and Microgastrinae (Maetô 1996), the cuspis and digitus freely articulate, and there are about 10 very small teeth distally on the digitus, as in some Cardiochilinae. The basal ring is longer than in most microgastrines (i.e., forms a broad transverse band), but shorter than in some derived microgastrine genera. Thus for the most part, mendeselline male genital capsules exhibit relatively plesiomorphic features, as would be expected from their proposed phylogenetic relationships (Whitfield and Mason 1994).

Mendesella orianae Valerio & Whitfield
sp. nov.
(Figs. 1b, 4)

Male.—Body color: Mainly honey yellow, with antennal flagellomeres as dark brown as inter-ocellar space; scape and pedicel light brown, metasomal terga 2–7 (except median area of tergum 2 and 3 whitish-yellow), hind tibia distal 1/5 and fore as middle leg telotarsus. First metasomal tergum with lateral areas yellow. Head, mesonotum and hind tibia with a darker tone of yellow than mesopleuron coloration; compound eyes silver; palpus whitish-yellow.

Fore and hind wing slightly infusate throughout; wing veins light brownish-yellow, except hind RS and 2M nebulo-se (with a short basal area tubular) with a dark brown coloration. Body length = 3.80 mm; Fore wing length = 3.19 mm. **Head:** head height/compound eye height = 1.25; head height/compound eye length = 1.67; length of first antennal flagellomere = 0.26 mm; length of first antennal flagellomere/width of first antennal flagellomere = 3.2; length of first antennal flagellomere/length of second antennal flagellomere = 1.33; length of first antennal flagellomere/length of third antennal flagellomere = 1.45; distal flagellomere length/width of distal flagellomere = 3.0; intertentorial pit distance = 0.18 mm; ocell-ocular distance = 0.05 mm; distance between toruli and tentorial pits = 0.28 mm; face wide at dorsal edge of clypeus = 0.36 mm. Antenna with 38 flagellomeres, distal flagellomere with a long and thick spine; face, frons, vertex, gena (except ventral area) densely punctate; clypeus mainly nitid, with scattered punctate sculpturing present; malar suture present; malar space very short; ocelli forming an equilateral triangle. **Mesosoma:** mesosomal length/mesosomal width = 1.64, mesosomal height = 0.82 mm; hindtibial length/hindtibial width = 3.5; Pronotal lateral areas with few obscure longitudinal lineate sculpturing; mesonotum evenly punctate throughout as setose; notaulus foveate anteriorly, remainder with obscure foveate sculpturing; area at notaulus union with rugulo-punctate sculpturing in a depressed area; union of notaulus near transscutal articulation; mesopleuron nitid, setose ventrally and remainder scattered setose; sternaulus obscurely impressed and nitid; transscutal articulation with a smooth carina; scutellar sulcus deep and wide, with 9 conspicuous pits present; scutellum subpentagonal, with two subrectangular pits close to one another at posterior apico-median area; antero-medial area of metanotum with two

subcircular pits near scutellar subrectangular pits, distal edge punctate throughout; axillary troughs of mesonotum with coarsely-rugose sculpturing; propodeum with parallel mid-longitudinal carinae united by transversal carinae between them, remainder with areolate-rugulose sculpturing present, latero-longitudinal carinae as cristate as mid-longitudinal carinae (no other carinae as strongly cristate). **Metasoma:** Distal width of tergum 1/Basal width of tergum 1 = 1.10; Length of tergum 1/Distal width of tergum 1 = 2.11; first metasomal tergum, dorso-lateral carinae strong, dorsal carinae curving close to another apically and not conspicuously cristate, rugulose sculpturing throughout tergum, medial area raised forming two semicircular lower areas that contain 5 costulae each; terga 2–6 smooth and unsculptured; tergum 2 with a "E" shaped form, the mid-dorsal part as strongly sclerotized as lateral areas of it, but not reaching half of the length of the tergum.

Holotype.—Costa Rica, Guanacaste, Parque Nacional Guanacaste, Estac. Los Almendros, 300 m. 23/iii-28/iv/1994, Col. E. López. Deposited in INBio.

Comments.—This species is similar to *Mendesella magna* and *M. braziliensis*, both described by Whitfield & Mason (1994), but can be separated from them by the absence of two elongated mid-lateral pits on the first metasomal tergum, by metasomal tergum 2 having an "E" shaped form with the mid-dorsal area as strongly sclerotized as the lateral areas, and the presence of rugulose sculpturing throughout the first metasomal tergum. Also, *M. oriana* can be separated from any other *Mendesella* species by the fore wing pattern of very weak infuscation, the mesopleuron and pronotum not being darkened, the smaller body size, and the darker metasomal terga 3–6.

Etymology.—Gender: feminine. The present species is named in honor of Oriana Valerio Contreras; live longer and prosper!

DISCUSSION

At present, the appearance of *Mendesella oriana* in Costa Rica expands the northern limit of known distribution for the genus *Mendesella*. Until now, the genus was reported only from Brazil, Bolivia and Ecuador (Whitfield & Mason 1994) with no observed specimens of the genus in the Caribbean zone of America. In contrast, the genus *Epsilogaster* has a reported northern limit of the southern U.S. (including the Caribbean area), with a southern limit in Brasil. The present observed sparse distribution is likely to be the result of the lack of specimens collected in other areas, in combination with the difficulty of identifying braconid wasps.

ACKNOWLEDGMENTS

We would like to thank The Instituto Nacional de Biodiversidad (INBio) for the loan of their mendeselline material. Thanks also to Axel Retana for his accurate comments, to Andy Deans for his help in the wing drawing technique, to "la canalla biológica de la calle de la perdición" in Costa Rica for their constant support, and of course to "Cukha" for her unconditional presence.

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Revision of the Enigmatic Genus *Marshiella* Shaw in the New World with the Description of Three New Species (Hymenoptera: Braconidae: Euphorinae)

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Abstract.—The genus *Marshiella* Shaw is revised for the New World region. Included are two previously described species, *Marshiella plumicornis* (Ruthe) and *M. pulvilicornis* (Walley and MacKay), and three newly described species, *M. bobella* Shaw, *M. lettermani* Shaw, and *M. marshi* Marsh. A key to New World species is provided, along with species descriptions, diagnostic characters, distribution, antennal micromorphology, and phylogenetic patterns.

The euphorine braconid genus *Marshiella* was erected by Shaw (1985) to include two enigmatic species with unusually modified antennae that had previously been placed in other genera. *Marshiella plumicornis* (Ruthe) was formerly placed in *Microctonus* Wesmael (Shenefelt 1969), while *M. pulvilicornis* (Walley and MacKay) was previously placed in *Streblocera* Westwood (Walley and MacKay 1963), but Shaw (1985) demonstrated that these species were closely related based on the uniquely modified, densely setose basal flagellomeres (Figs. 1–2) and must be assigned to a new genus. Previously the genus was known only from the Holarctic region, extending as far south as Mexico in the New World (Shaw 1985). More recently the genus has been recorded as far south as Costa Rica (Shaw 1997) and two new species have been recently described from China (Chen and van Achterberg 1997) extending the known distribution to the Oriental region. In this paper the New World species are reviewed and three new species are described including material from Arizona, Texas, Mexico, Costa Rica, and Brazil.

A full generic diagnosis for the genus *Marshiella* has been published by Shaw (1985) and more recently by Chen and van Achterberg (1997), so it is not necessary to repeat that information here. Recognition of the genus is quite easy as it is the only braconid with flagellomeres 1–4 or 1–5 flattened and densely setose ventrally (as in Figs. 1–2, 5–6, 10–16, 18–19). Specimens can be keyed to genus using the keys provided by Shaw (1985), Chen and van Achterberg (1997), or Shaw (1997).

Very little is known about the biology of *Marshiella* species, but they are presumed to be koniobiont endoparasitoids of adult Coleoptera as are most other basal clades of the Euphorinae (Shaw 1985, 1988; Shaw and Huddleston 1991). Only one species, *M. plumicornis* (Ruthe) has been reared from a host, an anthicid beetle, *Notoxus monoceros* L. (Smith 1953; Gornitz 1937). The same species has been collected at cantharadin-baited traps in Michigan, indicating that *Marshiella* species probably orient to their hosts using chemical cues (Shaw 1985; Dettner 1997). Mostly *Marshiella* species are quite rare, with

the Canadian species *M. pulvilicornis* (Walley and MacKay) and the two Chinese species, *M. binarius* Chen and van Achterberg and *M. sinensis* Chen and van Achterberg, being known only from the holotypes. However, two of the new species treated in this paper have been collected in series from Malaise traps in Costa Rica, and occasionally are attracted to lights. Males are totally unknown. The function of the modified flagellum in *Mar-*

shiella females has not been observed, but its form suggests the possibility that it is an adaptation for grasping the host beetle during oviposition since female euphorines oviposit by swinging the metasoma ventrally and anteriorly and exerting the ovipositor forward between the legs and in front of the face of the advancing wasp.

Authorship for new species is by either Shaw or Marsh, as indicated for each species.

KEY TO THE FEMALES OF NEW WORLD SPECIES OF *MARSHIELLA* SHAW

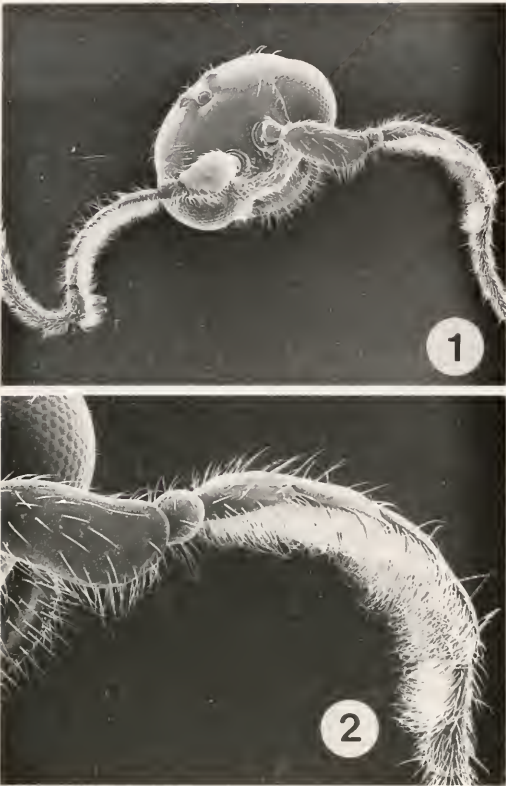
1. Dorso-lateral areas of propodeum entirely rugulose (Fig. 3); flagellomeres 2–4 in dorsal view only slightly broader than flagellomeres 8–10 *Marshiella plumicornis* (Ruthe)
- Dorso-lateral areas of propodeum entirely smooth and highly polished (Fig. 4); flagellomeres 2–4 in dorsal view strongly widened and heart-shaped (Figs. 5–6), about 2× broader than flagellomeres 8–10 2
2. Flagellomere 5 in dorsal view nearly cylindrical, and only slighter wider than flagellomere 6, not strongly flattened 3
- Flagellomere 5 in dorsal view strongly flattened, distinctly heart-shaped and nearly 2× broader than flagellomere 6 4
3. Body size very small, less than 2 mm long; antenna short, with only 17 flagellomeres; mesosoma reddish brown; known only from Canada *Marshiella pulvilicornis* (Walley and MacKay)
- Body size larger, more than 2 mm long; antenna longer, with 19–21 flagellomeres; mesosoma jet black; known only from Costa Rica *Marshiella lettermani* Shaw, new species
4. Metasomal tergum 1 entirely smooth on posterior half, beyond spiracles; ocellar-ocular space pale yellowish white; known only from Brazil *Marshiella marshi* Marsh, new species
- Metasomal tergum 1 finely rugulose on posterior half, beyond spiracles; ocellar-ocular space entirely or partly dark chocolate brown to black; know from Arizona, Texas, Mexico, and Costa Rica *Marshiella bobella* Shaw, new species

Marshiella bobella Shaw, new species

(Figs. 1–2, 4, 6, 8, 12–13)

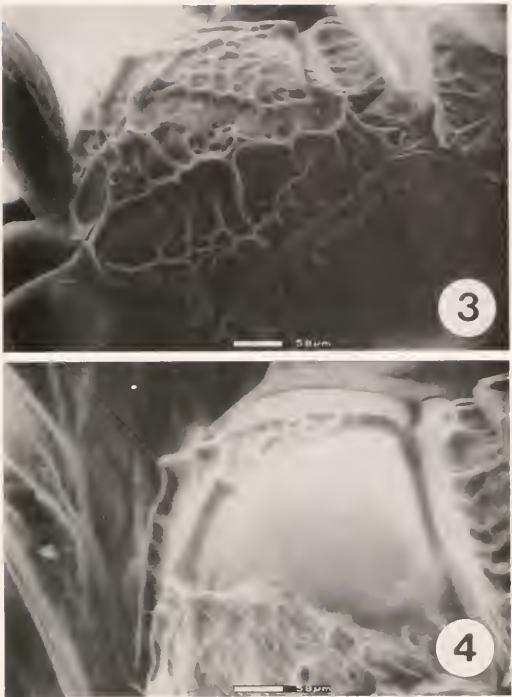
Description of holotype female.—Body length 2.3 mm; forewing length 2.3 mm; ovipositor length 1.1 mm. **Color:** frons, vertex, temple, and entire mesosoma black; flagellomeres 1–5 dorsally, remainder of flagellum, wing venation, entire metasoma and ovipositor sheath dark chocolate brown; scape, pedicel, flagellomeres 1–5 ventrally, remainder of head, legs entirely, and ovipositor light yellowish brown; eye silvery gray; wing mem-

brane hyaline; setae, especially on flagellomeres 1–5 ventrally, pale silvery white. **Head:** scape 2.3× longer than wide, apical ventral margin protruding and carinate longitudinally; flagellomeres 1–5 modified, pulvilliform, heart-shaped in dorsal view, ventrally densely setose with long wispy setae (Figs. 12–13); flagellomere 1 2× longer than wide; flagellomere 2 about as long as wide; flagellomeres 3–4 slightly wider than long; flagellomere 5 smaller, about as long as wide; remainder of flagellum comprising 15 flagellomeres of



Figs. 1-2. *Marshiella bobella* Shaw, anterior view. 1, head and antennae. 2, basal section of antenna showing modified flagellomeres 1-5.

normal form; face somewhat protruding below antennal insertions; eyes convergent ventrally, closest near mid-point of face; ocelli small, ocellar-ocular distance 5× width of lateral ocellus. **Mesosoma:** mesoscutum smooth and highly polished except notauli finely foveate, lateral lobes mostly devoid of setae; scutellar furrow 2-foveate; scutellar disc and dorso-lateral faces of propodeum smooth and highly polished; mesopleuron smooth and highly polished except smooth and finely foveate sternaulus; length of marginal cell 0.6× length of pterostigma; smooth dorso-lateral surfaces of propodeum margined posteriorly by V-shaped carinae; posterior surface of propodeum slightly depressed medially, margined laterally by carinae; median line of propodeum, posterior, and lateral surfaces rugulose, but polished and



Figs. 3-4. Propodeum, dorso-lateral view, 220×. 3, *Marshiella plumicornis* (Ruthe). 4, *Marshiella bobella* Shaw.

shining. **Metasoma:** petiolate tergum 1 narrow basally, then gradually wider, posterior width 3× wider than extreme basal width; petiole 7× longer than wide at extreme base; dorsal surface of petiole finely longitudinally rugose; remainder of metasoma smooth and highly polished; ovipositor length 2× length of tergum 1, basally emerging from longitudinal ventral slit about at mid-point of metasoma below tergum 3, widely separated from base of ovipositor sheath.

Variation.—paratype females appearing similar to holotype except apical 'normal' section of flagellum with 14 or 15 flagellomeres. The ovipositor is extremely flexible and varies in appearance depending on its position at death. Ovipositor shape varies from curved along basal ½ to nearly straight. Depending on the degree to which the tip of the metasoma is flexed ventrally and anteriorly the ovipositor base may appear to emerge apically or

ventrally near the mid-point of the metasoma. The specimens from Texas have less dark brown color on the top of the head, but otherwise agree with the diagnosis of this species.

Material examined.—Holotype female: Costa Rica, San Jose Province: Zurqui de Moravia, 1600 m, April 1992, P. Hanson, Malaise trap, deposited at University of Wyoming. Paratype females: 1 same data as holotype; 1 same data except July 1990; 6 same data except November–December 1990; 1 same data except May 1992; 3 same data except June 1992; 1 same data except July 1992; 1 same data except February 1996. Cartago Province: 1, La Cangreja, 1950m, July 1991, P. Hanson, Malaise trap; 1 same data except June–July 1992. Guanacaste Province: 1, P. N. Guanacaste, 9 km S Santa Cecilia, Estacion Pitilla, 700 m, 2–19 March 1992, P. Rios, INBio barcode CR1000–420531; 1 same data except 31 March–15 April 1992, INBio barcode CR1000–771575; 1, Tierras Morenas, 700m, December 1992, G. Rodriguez, INBio barcode CR1001–288145; 1, Santa Rosa National Park, 300 m, 14 August–6 September 1986, I. D. Gauld and D. Janzen, Malaise trap, Bosque Humedo, mature evergreen dry forest, fully shaded. Mexico: 1, Chis., L. Montebello National Park, 5000 ft., 30 May 1969, Malaise trap. U.S.A.: 1, Arizona, 5 mi. W Portal, 7 July 1956, O. L. Cartwright, light trap; 2, Texas, Sabine Co., 9 mi. E. Hemphill, 23 June to 2 July 1989, Anderson and Morris, flight intercept trap in beech/magnolia forest. Paratypes deposited at University of Wyoming, Universidad de Costa Rica, Instituto Nacional de Biodiversidad, Texas A&M University, and U.S. National Museum of Natural History.

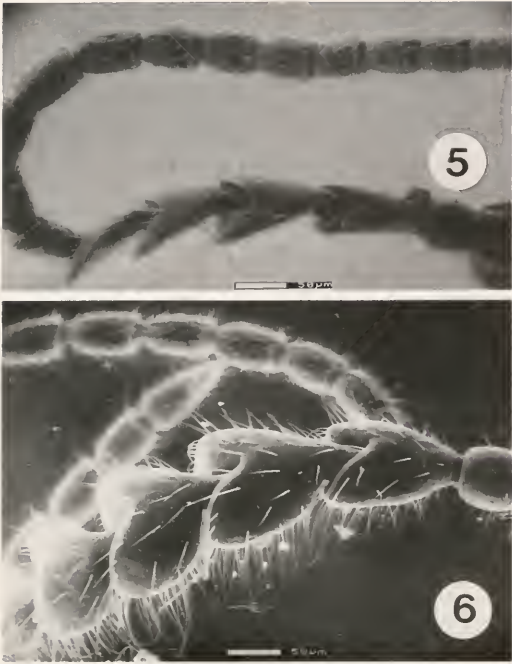
Comments.—Specimens of this species from Arizona and Mexico had been previously treated as variations of *M. pulvillicornis* by Shaw (1985), but the substantial series of specimens now available from Costa Rica show this to be a distinct species most easily separated by its having

flagellomere 5 modified along with flagellomeres 1–4, larger body size, and longer flagellum. The only other *Marshiella* species with flagellomere 5 modified is *Marshiella marshi* from Brazil, which can be distinguished by its smooth metasomal tergum 1 and lighter head color.

Etymology.—The species name is an arbitrary combination of letters to form a euphonious combination.

***Marshiella lettermani* Shaw, new species**
(Figs. 14–16)

Description of holotype female.—Body length 2.9 mm; forewing length 2.8 mm; ovipositor length 1.3 mm. **Color**: frons medially, ocellar triangle, and entire mesosoma except prosternum black; flagellomeres 1–4 dorsally, remainder of flagellum, prosternum, wing venation, entire metasoma and ovipositor sheath dark chocolate brown; scape, pedicel, flagellomeres 1–4 ventrally, remainder of head, legs entirely, and ovipositor very pale yellowish brown; eye silvery gray; wing membrane hyaline; setae, especially on flagellomeres 1–5 ventrally, pale silvery white. **Head**: scape 2.3× longer than wide, apical ventral margin protruding and carinate longitudinally; flagellomeres 1–4 modified, pulvilliform, heart-shaped in dorsal view, ventrally densely setose with long wispy setae on flagellomeres 1 and 4, shorter bent Velcro-like setae on flagellomeres 2–3 (Figs. 14–16); flagellomere 1 2× longer than wide; flagellomere 2 about as long as wide; flagellomere 3 slightly wider than long; flagellomere 4 smaller, about as long as wide; remainder of flagellum comprising 17 flagellomeres of normal form; face somewhat protruding below antennal insertions; eyes convergent ventrally, closest near mid-point of face; ocelli small, ocellar-ocular distance 3.5× width of lateral ocellus. **Mesosoma**: mesoscutum smooth and highly polished except notauli finely foveate, lateral lobes mostly devoid of setae; scutellar furrow 2-foveate; scutellar

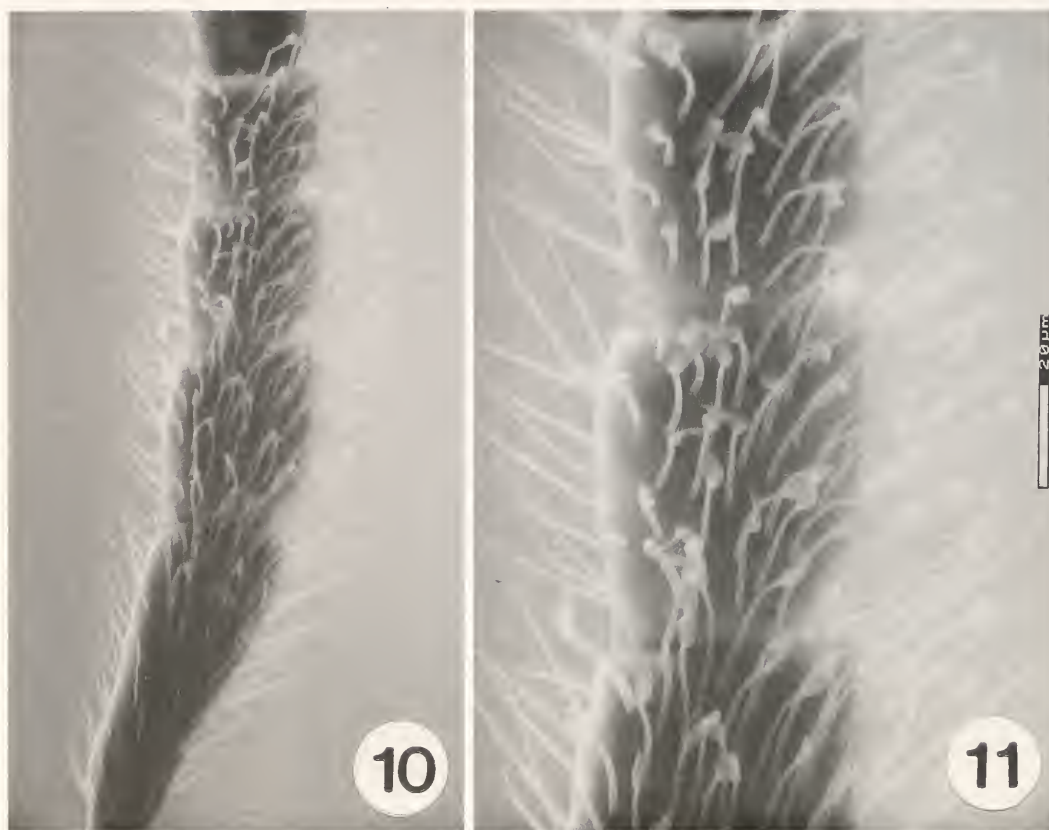


Figs. 5–6. Basal section of antennal flagellum, dorso-lateral view. 5, *Marshiella pulvilicornis* (Walley and MacKay), 230 \times . 6, *Marshiella bobella* Shaw, 235 \times .

disc and dorso-lateral faces of propodeum smooth and highly polished; mesopleuron smooth and highly polished except smooth and coarsely-foveate sternaulus; length of marginal cell 0.9 \times length of pterostigma; smooth dorso-lateral surfaces of propodeum margined posteriorly by V-shaped carinae; posterior surface of propodeum slightly depressed medially, margined laterally by carinae; median line of propodeum, posterior, and lateral surfaces rugulose, but polished and shining. **Metasoma:** petiolate tergum 1 narrow basally, then gradually wider, posterior width 2.8 \times wider than extreme basal width; petiole 6 \times longer than wide at extreme base; dorsal surface of petiole finely longitudinally rugose on basal 3/4; posterior 1/4 of petiole and remainder of metasoma smooth and highly polished; ovipositor length 1.9 \times length of tergum 1, basally emerging from longitudinal ventral slit about at mid-point of metasoma below tergum 3, widely separated from base of ovipositor sheath.



Figs. 7–9. Metasomal tergum 1, dorso-lateral view. 7, *Marshiella plumicornis* (Ruthe), 220 \times . 8, *Marshiella bobella* Shaw, 195 \times ; 9, *Marshiella marshi* Marsh, 220 \times .



Figs. 10–11. *Marshiella plumicornis* (Ruthe), basal section of antennal flagellum, ventral view. 10, flagellomeres 1–5, 295 \times . 11, detail of flagellomeres 1–3 showing spatulate setae, 700 \times .

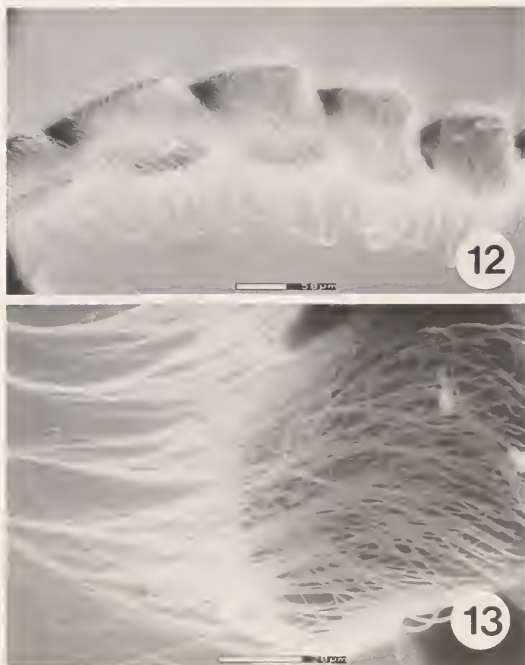
Variation.—paratype females appearing similar to holotype except apical 'normal' section of flagellum with 15 to 17 flagellomeres, body size 2.2 to 2.9 mm, and dark brown covering most of frons and vertex.

Material examined.—Holotype female: Costa Rica, Puntarenas Province: San Vito, Estacion Biologica Las Alturas, 1500 m, December 1991, P. Hanson, Malaise trap, deposited at University of Wyoming, Laramie. Paratype females: 1 same data as holotype; 1 same data except November 1991; 2 same data except June 1992. Paratypes deposited at University of Wyoming and Universidad de Costa Rica.

Comments.—*Marshiella lettermani* is most similar to *M. pulvilicornis* (Walley and MacKay) in that both of these species have

flagellomeres 1–4 greatly widened and densely setose, but flagellomere 5 is not so modified. The Costa Rican species *M. lettermani* can be distinguished from *M. pulvilicornis* by its larger body size (nearly 3 mm), black mesosoma, short bent Velcro-like setae on flagellomeres 2–3 (Fig. 16), and longer flagellum with 19–21 flagellomeres. *M. pulvilicornis* is much smaller (less than 2 mm), has a reddish brown mesosoma, shorter flagellum with only 17 flagellomeres, entirely long wispy flagellar setae, and is known only from Canada.

Etymology.—The species name is a patronym for David Letterman, host of the Late Show, in appreciation for his outstanding contributions to late night entertainment. Many a dull day has been im-



Figs. 12–13. *Marshiella bobella* Shaw, basal section of antennal flagellum, ventral view. 12, flagellomeres 1–5, 215 \times . 13, detail of flagellomere 5 showing long wispy setae, 905 \times .

proved by his humor. It somehow seems appropriate that a really weird insect should be named in his honor.

***Marshiella marshi* Marsh, new species**
(Figs. 9, 17–19)

Description of holotype female.—Body length 2.9 mm; forewing length 2.8 mm; ovipositor length 1.2 mm. **Color:** frons, vertex, and temple medially light brown; margins of ocelli and notauli black; flagellomeres 1–5 dorsally, remainder of flagellum, wing venation, mesosoma except prosternum, metasoma except petiole basally, and ovipositor sheath dark reddish brown; scape, pedicel, flagellomeres 1–5 ventrally, remainder of head, legs entirely, and ovipositor very pale yellowish brown to yellowish white; eye silvery gray; wing membrane hyaline; setae, especially on flagellomeres 1–5 ventrally, pale silvery white. **Head:** scape 3.0 \times longer than wide, apical ventral margin protruding (Fig. 17)

and carinate longitudinally; flagellomeres 1–5 modified, pulvilliform, heart-shaped in dorsal view, ventrally densely setose with long wispy setae, some of which are intertwined or braided (Figs. 18–19); flagellomere 1 1.5 \times longer than wide; flagellomere 2 about as long as wide; flagellomeres 3–4 slightly wider than long; flagellomere 5 smaller, about as long as wide; remainder of flagellum comprising 15 flagellomeres of normal form; face somewhat protruding below antennal insertions; eyes convergent ventrally, closest near mid-point of face; ocelli small, ocellar-ocular distance 4 \times width of lateral ocellus.

Mesosoma: mesoscutum smooth and highly polished except notauli finely foveate, lateral lobes mostly devoid of setae medially; scutellar furrow 2-foveate; scutellar disc and dorso-lateral faces of propodeum smooth and highly polished; mesopleuron smooth and highly polished except smooth and finely-foveate sternaulus; length of marginal cell 0.7 \times length of pterostigma; smooth dorso-lateral surfaces of propodeum margined posteriorly by V-shaped carinae; posterior surface of propodeum slightly depressed medially, margined laterally by carinae; median line of propodeum, posterior, and lateral surfaces rugulose, but polished and shining. **Metasoma:** petiolate tergum 1 narrow basally, then gradually wider, posterior width 3 \times wider than extreme basal width; petiole 7 \times longer than wide at extreme base; dorsal surface of basal 1/2 of petiole finely longitudinally rugose; posterior 1/2 of petiole and remainder of metasoma smooth and highly polished; ovipositor length 2 \times length of tergum 1, basally emerging from longitudinal ventral slit about at mid-point of metasoma below tergum 3, widely separated from base of ovipositor sheath.

Material examined.—Holotype female: Brazil, Rondonia, Vilhena, 21 degrees 40 minutes S, 60 degrees 08 minutes W, October 1973, M. Alvarenga, deposited at Canadian National Collection, Ottawa.



Figs. 14–16. *Marshiella lettermani* Shaw, basal section of antennal flagellum, ventral view. 14, flagellomeres 1–5, 215 \times . 15, flagellomeres 3–4, 745 \times , showing variation of seta form and density. 16, flagellomere 3, 1450 \times , showing detail of short, bent, Velcro-like setae.

Comments.—*Marshiella marshi* can be separated from most other species by its having flagellomere 5 modified along with flagellomeres 1–4, larger body size, and longer flagellum. The antennal scape is slightly more protruberant and setose (Fig. 17) than other species. Some of the long wispy setae on flagellomeres 2–3 are intertwined or braided (Fig. 18–19), but the sample size is too limited to determine if this is natural or a post-mortem effect of preservation methods. The only other *Marshiella* species with flagellomere 5 modified is *M. bobella* from Arizona, Costa Rica, and Mexico, which can be distinguished from *M. marshi* by its rugulose metasomal tergum 1 and darker head color.

Etymology.—The species is named in honor of Jon Marsh, son of the junior author.

***Marshiella plumicornis* (Ruthe)**
(Figs. 3, 7, 10–11)

Microctonus plumicornis Ruthe, 1856. Reclassified by Shaw, 1985.

Description of female based on North American material.—Body length 1.8–1.9 mm;

forewing length 1.7–1.8 mm; ovipositor length 0.6–0.7 mm. **Color:** frons, vertex, temple, gena, mesosoma except pronotum and prosternum, flagellomeres 4–16, wing venation, entire metasoma and ovipositor sheath dark chocolate brown to black (fading to yellowish brown in old specimens); scape, pedicel, flagellomeres 1–3, remainder of head, legs entirely, and ovipositor light yellowish brown; eye silvery gray; wing membrane hyaline; setae, especially on flagellomeres 1–4 ventrally, pale silvery white. **Head:** scape 2.2 \times longer than wide, apical ventral margin not protruding or carinate longitudinally; flagellomeres 1–4 modified, pulvilliform, narrowly heart-shaped in dorsal view, ventrally densely setose with setae expanded and flattened apically into spatulate tips (Figs. 10–11); flagellomere 1 3 \times longer than wide; flagellomeres 2–3 about 2 \times as long as wide; flagellomere 4 1.5 \times wider than long; remainder of flagellum comprising 12 flagellomeres of normal form; face not protruding below antennal insertions; eyes convergent ventrally, closest near ventral margin of face; ocelli small, ocellar-ocular distance 5 \times width of lateral



Figs. 17–19. *Marshiella marshi* Marsh, basal section of antenna. 17, scape and pedicel, lateral view, 380 \times . 18, flagellomeres 1–5, ventral view showing long wispy setae, 250 \times . 19, flagellomere 2, ventral view showing detail of intertwined, braided setae, 885 \times .

ocellus. **Mesosoma:** mesoscutum smooth and highly polished except notauli foveate, median and lateral lobes mostly devoid of setae; scutellar furrow 2-foveate; scutellar disc smooth and highly polished; mesopleuron smooth and highly polished except coarsely-foveate sternaulus; length of marginal cell 0.4 \times length of pterostigma; rugulose dorso-lateral surfaces of propodeum margined posteriorly by V-shaped carinae; posterior surface of propodeum slightly depressed medially, margined laterally by carinae; median line of propodeum, dorso-lateral, posterior, and lateral surfaces rugulose, but somewhat polished and shining. **Metasoma:** petiolate tergum 1 narrow basally, then gradually wider, posterior width 3 \times wider than extreme basal width; petiole 5 \times longer than wide at extreme base; dorsal surface of petiole finely longitudinally rugose; remainder of metasoma smooth and highly polished; ovipositor length 1.6 \times length of tergum 1, basally emerging from longitudinal ventral slit apically to near midpoint of metasoma below tergum 3, widely separated from base of ovipositor sheath.

Material examined.—U.S.A., Arizona: 1

female, Safford, 4 November 1955, G. D. Butler, swept from alfalfa. California: 1 female with cocoon, Chino, July 1932, A. J. Basinger, ex. peaches infested by *A. lineatella*. Florida: 1 female, St. Lucie Co., 31 March–5 April 1930, J. R. Barass, Florida fruit fly trap survey; 1 female, Indian River, 10 March 1930, J. R. Barass, Florida fruit fly trap survey. Michigan: 2 females, Ingham Co., Dewitt Township, 10–17 June 1982, D. K. Young, taken at cantharadin bait. 1 female, Kalamazoo Co., Harrison Lake, T3S, R12W, sec. 34, 16–26 June 1982, J. K. Young, taken at cantharadin bait. South Carolina: 1 female, Clemson, no date, G. G. Ainslie; 1 female, Clio, 22 July 1936, on cotton, lot 36–30265. Deposited at U.S. National Museum of Natural History, Washington, D.C. Holotype female from Germany examined by Shaw (1985), deposited at the Natural History Museum, London.

Comments.—This species has the widest distribution of any *Marshiella* species, being recorded from both Europe (Chen and van Achterberg 1997) and the United States (Shaw 1985). *M. plumicornis* can be easily distinguished from all other New World species of *Marshiella* by the dorso-

lateral areas of the propodeum being entirely rugulose and flagellomeres 2–4, in dorsal view, being only slightly wider than flagellomeres 8–10.

The distinctive flagellar setae micromorphology (Figs. 10–11), with the ventral setae of flagellomeres 1–4 having flattened, spatulate tips, was previously documented by Shaw (1985). It was previously presumed that this setal micromorphology was a characteristic of the genus *Marshiella* (Shaw 1985; Chen and van Achterberg 1997), however, the more complete survey presented here indicates that setal micromorphology varies among *Marshiella* species, and the spatulate form has so far only been documented in *M. plumicornis*.

Biology.—*M. plumicornis* has been reared from the anthicid *Notoxus monoceros* L. in Europe (Gornitz 1937; Smith 1953), but it has not yet been reared in North America. It has been attracted to cantharadin bait (Shaw 1985), suggesting possible chemosensory location of coleopteran hosts (Dettner 1997). Dan Young (pers. comm.) reports having seen braconids attracted to cantharadin in Michigan (presumably this species) attacking anthicids near the trap. One specimen was reared from peaches infested with the gelechiid *Anarsia lineatella* Zeller (the peach twig borer), but it seems unlikely that this was the actual host (more likely it was a beetle in the same substrate).

***Marshiella pulvillicornis* (Walley and MacKay)
(Fig. 6)**

Streblocera pulvillicornis Walley and MacKay, 1963. Reclassified by Shaw, 1985.

Material examined.—Holotype female, Canada, Quebec, Gatineau Park, Meach Lake, 9 June 1961, G.S. Walley, sweeping, No. 8223, deposited in Canadian National Collection, Ottawa.

Comments.—This species was described by Walley and MacKay (1963) based on a single female specimen from Quebec. No new material of the species has since been

discovered, therefore there is no need to redescribe the species here. In addition to other characters mentioned in the key, this species can be distinguished from other *Marshiella* by its small body size (less than 2mm), short flagellum with 17 flagellomeres, and reddish brown mesosoma.

Discussion of Phylogenetic Considerations.—Our understanding of variation for characters of possible phylogenetic significance in *Marshiella* species is no doubt limited by the scarcity of material for several species, and also the lack of biological data for all but one species. Nevertheless, it is tempting to speculate on the possible phylogenetic interpretation of several characters, especially the unique antennal modifications which are presumptive synapomorphies by out-group comparison with the presumed sister-group, *Townesililus* (Shaw 1985).

Four of the New World species appear to form a distinctive monophyletic cluster including *M. bobella*, *M. lettermani*, *M. marshi*, and *M. pulvillicornis*. Synapomorphies supporting this lineage include greatly widened and strongly flattened basal flagellomeres (Fig. 18), modified scape with the apical ventral margin protruding (Fig. 17), dorsum of propodeum with large smooth areas devoid of sculpture (Fig. 4), and face with pale coloration. Although the two Chinese species were not available for examination, the published descriptions agree more closely with the conditions seen in the more basal *M. plumicornis* which has more cylindrical and less flattened flagellomeres, shorter and less protruding scape, rugose propodeum, and brown face. The significance of a derived cluster including *M. bobella*, *M. lettermani*, *M. marshi*, and *M. pulvillicornis* is two-fold. First, this indicates that all the more basal species of *Marshiella* have holarctic or palearctic distributions, while all the species with Neotropical distributions belong to a derived strictly New World cluster. This is consistent with an hypothesis of one invasion of South America, from the north

temperate zone. Second, it shows that the one species with known biology is basal, suggesting the possibility that the highly modified antennae of the more southern New World species may also be modifications for locating hosts via cantharadin or other semiochemicals.

ACKNOWLEDGMENTS

Special thanks to Prof. Paul Hanson, of the Universidad de Costa Rica, for running the Malaise Trap network over many years, which yielded most of the Costa Rican material treated here. Specimens were also provided by the Canadian National Collection, Ottawa, the Instituto Nacional de Biodiversidad (IN-Bio), Heredia, and the U.S. National Museum of Natural History, Washington, D.C. Thanks to Prof. Dan Young, of the University of Wisconsin, for sharing his observations on braconids attracted to cantharadin.

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Description of a New Gregarious Species of *Aleiodes* Wesmael (Hymenoptera: Braconidae: Rogadinae)

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Abstract.—*Aleiodes leptocarina* Fortier, a new species from Costa Rica, is described and illustrated. Specimens were reared from a large lepidopteran caterpillar, making this species one of only three presently known gregarious *Aleiodes* species. Morphological comparisons are made with *A. stigmator*, the other New World gregarious species.

The rogadine braconid genus *Aleiodes* Wesmael is worldwide in distribution (Shaw *et al.* 1997). Fortier and Shaw (1999) list 208 *Aleiodes* species worldwide. Evidence (Fortier, unpublished data) suggests that it may be far more species-rich in the Neotropics than had heretofore been known.

Species of tribe Rogadini, to which *Aleiodes* belongs, are koinobiont endoparasitoids of more or less exposed lepidopteran larvae (Shaw 1983, 1994; Shaw and Huddleston 1991; Shaw 1995, Fortier and Shaw 1999). A characteristic of Rogadini is that pupation takes place inside the dead host's larval skin, which hardens and darkens to become a 'mummy' (Shaw and Huddleston 1991).

Aleiodes host mummies can usually be distinguished from those of its putative sister group *Rogas* (Whitfield, 1992) in that 1) a slit is cut in the ventral area of the host's thoracic region, through which a sticky substance is emitted, which often functions to glue the mummy to a substrate, and 2) the emergence hole cut by the emerging adult parasitoid is normally less jagged and more circular as compared with *Rogas* (Shaw 1995, 1997; see Fig. 8 this paper).

Fortier and Shaw have argued that basal *Aleiodes* species tend to be less host specific while derived species tend to feed ex-

clusively on non-catocaline noctuids. They suggest an evolutionary pattern for koinobiont endoparasitoids in which more derived species tend to have narrower host ranges than less derived species (Fortier and Shaw 1999).

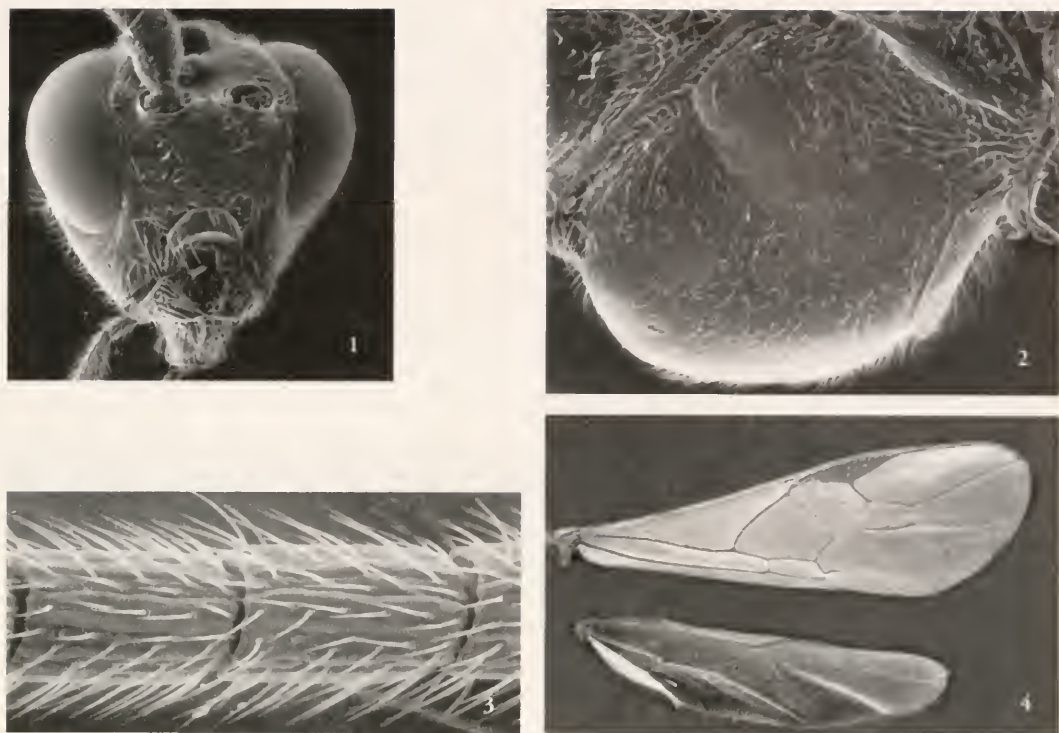
Evidence (Fortier and Shaw 1999) suggests a coevolutionary trend between *Aleiodes* and their lepidopteran hosts. Basal host families are more likely to be attacked by basal *Aleiodes* species while the most derived host family, Noctuidae, is more likely to be attacked by derived *Aleiodes* species.

So far as known previous to this study, only two *Aleiodes* species, a Palaearctic species and the Nearctic species *A. stigmator* (Say), are gregarious (Shaw and Huddleston 1991, Shaw 1997).

METHODS

This species can be identified as a member of the subfamily Rogadinae by using the keys of Shaw (1995), Shaw and Huddleston (1991), or Wharton *et al.* (1997). My definition of *Aleiodes* follows that of van Achterberg (1991), Fortier and Shaw (1999), Shaw (1993), and Shaw *et al.* (1997). Specimens can be determined as *Aleiodes* using the key of Shaw (1997).

Terminology follows that used by Shaw *et al.* (1997). Microsculpture terminology follows that of Harris (1979). Wing vein



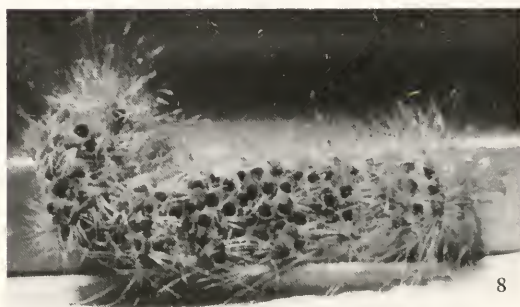
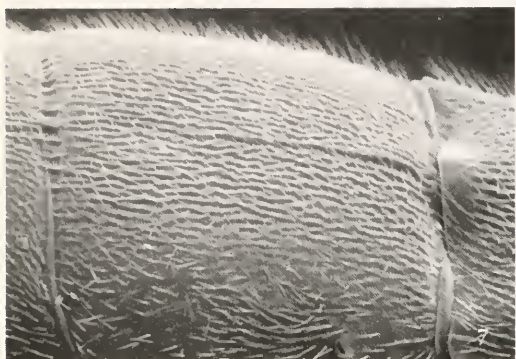
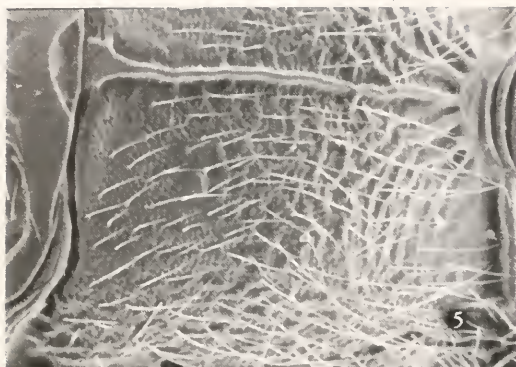
Figs. 1–4. *Aleiodes leptocarina*. 1, Head. 2, Mesopleuron. 3, Flagellomeres near middle of antenna. 4, Wings.

terminology agrees with that adopted by Wharton *et al.* (1997) and by Goulet and Huber (1993).

***Aleiodes leptocarina* Fortier, new species**
(Fig. 1–7)

Female.—**Body color:** honey yellow, legs and mandibles honey yellow except mandibular teeth and ocellar triangle black, clypeus occasionally with black; antennomeres dark honey yellow, wings hyaline, veins, stigma dark honey yellow. **Body length:** 6–7 mm; fore wing length, 5.5–6.0 mm. **Head:** 44–46 flagellomeres, first flagellomere length about 1.6 times width, 20th flagellomere length about 1.5 times width (Fig. 3); oral opening height slightly greater than or equal to width, clypeus protruding with distinct apical edge (Fig. 1); occipital carina interrupted at apex and not meeting hypostomal carina; ocelli moderately large, slightly

greater than ocell-ocular distance; face finely colliculate; longitudinal ridge between antennae occasionally extending down face up to 0.35 length of antenno-clypeal space; vertex colliculate; temples colliculate. **Mesosoma:** pronotum colliculate; mesonotum and scutellum colliculate; notauli without carinae; mesopleuron finely colliculate with a dull shine, subalar groove without carinae, sternaulus absent (Fig. 2); propodeum rugose or rugulose posteriad, faintly rugulose over colliculate surface anteriad, or without rugae (Fig. 5). **Legs:** tarsal claws of all legs completely pectinate (Fig. 6); hind coxae evenly colliculate dorsally and laterally. **Wings** (Figs. 4): hyaline; front wing vein r about half the length of 3RSa and about 1.3 times length of rm; vein 1CU-a about 0.8 length of 1CU-b; rear wing vein m-cu absent; RS slightly recurved, marginal cell narrowest at midpoint; vein r-m shorter than vein 1M; vein 1A meeting and terminating at



Figs. 5-8. *Aleiodes leptocarina*. 5, Propodeum. 6, Metatarsal claw. 7, Second metasomal tergite. 8, Dorsal view of host caterpillar.

apex of vein cu-a; vein M+CU over 1.5 times as long as vein 1M. **Metasoma:** metasomal tergite weakly rugulose, raised transverse carinae of first metasomal tergite at base joining medially to form median carina, median carina becoming fainter apically, first metasomal tergite length slightly less than or equal to apical width, basal width slightly greater than 0.5 apical width; second metasomal tergite weakly rugulose, median carina weak, occasionally absent in apical (Fig. 7); third metasomal tergite mostly shiny, finely colliculate with faint rugulation antero-medially, median carina usually absent basally, never present apically; tergites apical of third metasomal tergite smooth; ovipositor sheath length about 0.35 times basitarsis length.

Male.—Essentially as in female, except 41-43 flagellomeres, 20th flagellomere length over twice the width, forewing

length 5.0-5.5 mm., first metasomal tergite length slightly greater than apical width, third metasomal tergite weakly rugulose in basal half, weakly rugulose or shiny-colliculate in apical half, median carina occasionally weakly present in basal half.

Holotype.—Female: COSTA RICA, Cartago, P. N. Tapanti, 1150 m., LS194000, 559800, IX-5-1995, G. Mora, collector. Deposited in INBio.

Paratypes.—COSTA RICA: 76 females, 15 males, Cartago, P. N. Tapanti, 1150 m., LS194000, 559800, IX-5-1995, G. Mora, collector. Paratypes deposited in INBio, Wheeling Jesuit University Insect Collection, Texas A&M Department of Entomology Insect Collection, and Rocky Mountain Systematic Entomology Laboratory.

Distribution.—Known only from Costa Rica.

Biology.—Holotype and paratypes all reared from a single lepidopteran host

(Donald Davis, personal communication) (Fig. 8) about 7 cm. long.

Comments.—This species and *A. stigmator* (Say) are the only described gregarious New World species. The tarsal claw is closely similar to that of *A. stigmator* in arrangement of the pecten and in overall shape. This species differs from *A. stigmator* in having more than 34 antennomeres, clypeus protruding with distinct apical edge, shiny mesopleuron, finely reticulate rugulation on first and second metasomal tergites, and females with little or no rugulation on third metasomal tergite. Morphological features including short pronotum place it in the *gastritor* species-group. *A. stigmator* is also in this species-group (Fortier and Shaw 1999, Shaw *et al.* 1997). The clypeus protruding and edged apically is a derived character state found elsewhere in the *gastritor* species-group.

Etymology.—From the Greek *leptos* meaning “fine, delicate,” and *carina* meaning “ridge,” in reference to the finely reticulate rugulation on the first two metasomal tergites.

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Descriptions and Biological Notes on Two New Phytophagous Species of the Genus *Allorhogas* from Brasil (Hymenoptera: Braconidae: Doryctinae)

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Abstract.—Two new species of the genus *Allorhogas* are described from the Poço das Antas Biological Reserve, Rio de Janeiro State, Brasil: *A. spermaphagus* Marsh, reared from seed pods of *Stryphnodendron polyphyllum* (Leguminosae) and *A. brasiliensis* Marsh, reared from seed pods of *Pithecellobium pedicellare* (Leguminosae). Biological notes are provided and a key is presented to the species reared from plant seeds or galls in Brasil.

For centuries, species in the family Braconidae were thought to be always parasitoids of other insects. Macêdo and Monteiro (1989) presented the first documented case of phytophagy in the family Braconidae for a species of the braconid genus *Allorhogas* (subsequently described as *A. dyspistus* by Marsh 1991) which attacks seeds of the legume *Pithecellobium tortum* Martius in Brasil. Since then, more records of phytophagy in the Braconidae have been noted. Infante, et al. (1995) showed that species of the genus *Monitoriella* formed galls on *Philodendron* in Central and South America. Ramirez and Marsh (1996) described two species of the genus *Psenobolus* from Costa Rica which develop as inquilines in figs. Recently, Austin and Dangerfield (1998) showed that a species of the genus *Mesostoa* forms galls on *Banksia* in Australia and Macêdo et al. (1998) provided further information on the biology of *A. dyspistus* in Brasil. One of us (PMM) has seen a new species of *Allorhogas* from Costa Rica that has been reared from another species of *Pithecellobium*. Thus, it is now well established that phytophagy does occur in the family Braconidae.

For many years, there have been records of species in the genus *Allorhogas* being reared from plant galls but no firm biological data was available. For example, *A. galicola* Gahan was reared from oak galls (Gahan 1912) and *A. heringeri* (Guimarães) and *A. muesebecki* (Guimarães) were reared from plant galls (Guimarães 1957). No species have ever been definitely reared as parasitoids of other insects in galls or seed pods. As noted above and from the biological information presented here, it is now firmly established that species in the genus attack seed pods and are not parasitic on any other insect. Furthermore, several undescribed species from Costa Rica have been reared from various leaf galls, although no detailed biological studies have yet been made.

The following new species of the genus *Allorhogas* are described in order to provide names for further biological studies being done by two of us (MVM, MCPP). These species were reared from seeds of *Stryphnodendron polyphyllum* Martius and *Pithecellobium pedicellare* (DC.) Benth. in Brasil and preliminary observations are given under each species description be-

low. The genus is in need of study for the Neotropical Region. There are an estimated 50 species from Brasil, nearly all undescribed and mostly without biological information. A study is in progress on the genus from Costa Rica with an estimate of 25 undescribed species.

The names of the two new species are to be attributed only to the senior author; all biological observations were made by the junior authors. The genus *Allorhogas* can be identified by keys presented in Marsh (1997). Morphological terminology is based on Wharton, et al. (1997).

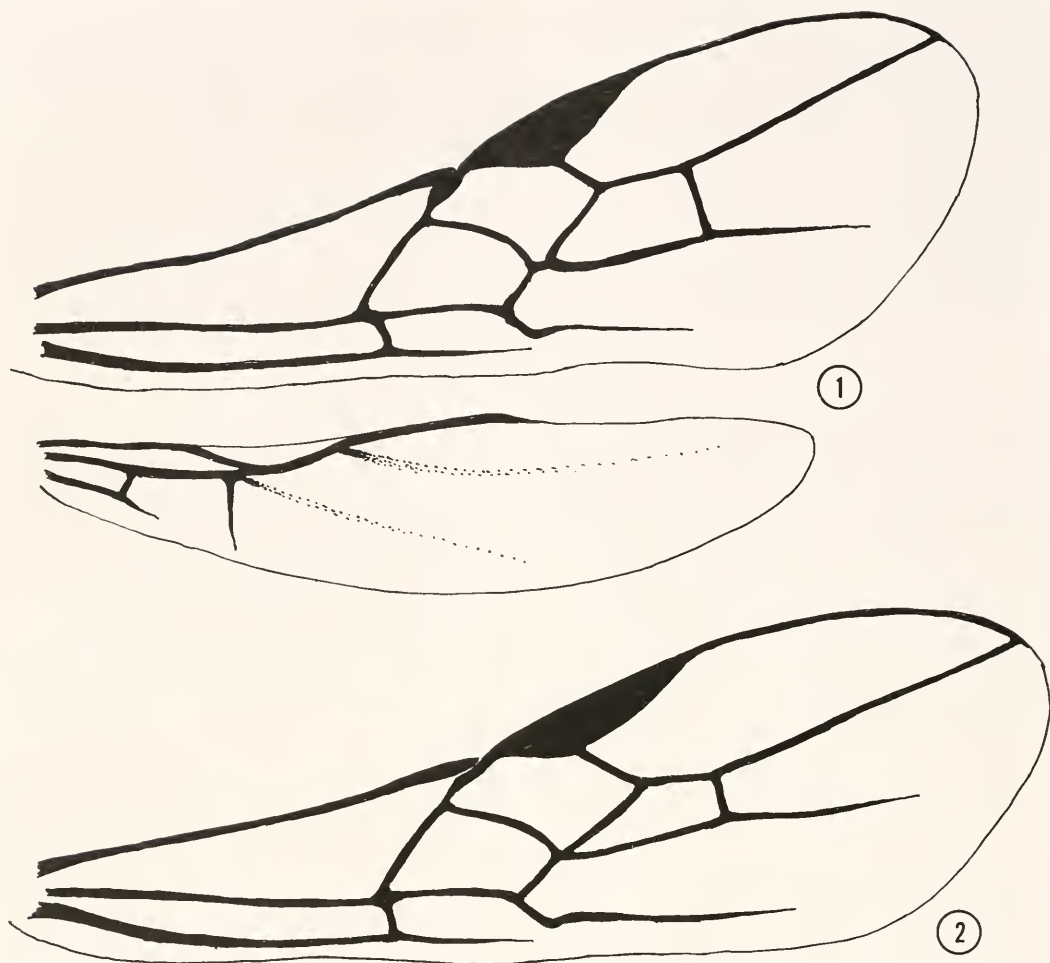
KEY TO SPECIES OF *ALLORHOGAS* REARED FROM PLANT SEEDS OR GALLS IN BRASIL
(Based on females only)

- 1. Ovipositor barely visible, shorter than first metasomal tergum 2
- Ovipositor at least half as long as metasoma 3
- 2(1). Malar space $2/5$ eye height *dyspistus* Marsh
- Malar space nearly equal to eye height *muesebecki* (Guimarães)
- 3(1). Fore wing vein m-cu arising distad of vein 2RS *heringeri* (Guimarães)
- Fore wing vein m-cu interstitial with or arising basad of vein 2RS 4
- 4(3). Fore wing vein m-cu interstitial with 2RS (Fig. 2); body length 3.50–3.75 mm; 29–30 antennomeres, flagellum light brown *spermaphagus* Marsh, new species
- Fore wing vein m-cu arising basad of 2RS, thus a short section of (RS+M)b present (Fig. 1); body length 4.0–4.5 mm; 34–35 antennomeres, flagellum honey yellow on basal $1/2$, brown on apical $1/2$ *brasiliensis* Marsh, new species

Allorhogas spermaphagus Marsh, new species
(Figs. 2–6)

Female.—**Body color**: head, mesosoma and metasoma honey yellow; legs yellow; flagellum and pedicel light brown; wings hyaline, fore wing vein C+Sc+R and stigma yellow, rest of veins light brown, hind wing veins yellow. **Body length**: 3.50–3.7 mm. **Head**: 29–30 antennomeres; face rugulose-coriaceous medially, strongly rugose along inner eye margins; frons excavated, coriaceous; vertex (Fig. 3) coriaceous, weakly rugulose behind ocelli; temple coriaceous; malar space $1/3$ eye height; oral opening small, circular, diameter equal to basal width of mandible; ocell-ocular distance twice diameter of lateral ocellus; occipital carina distinct, meeting hypostomal carina. **Mesosoma** (Figs. 4–5): pronotum weakly rugulose-coriaceous laterally with deep median scrobiculate groove bordered ventrally by carina; mesonotum sharply declivous anteriorly,

mesonotum and scutellum coriaceous, middle lobe with median scrobiculate groove extending to anterior edge of mesonotum; notauli distinctly scrobiculate, meeting in large rugose area before scutellum; scutellar furrow with three cross carinae; mesopleuron coriaceous, sternaulus deep and smooth or weakly scrobiculate; propodeum rugose, with two basolateral semicircular rugulose-coriaceous areas enclosed by carina, apical area above metasoma insertion usually smooth, enclosed by carina. **Legs**: fore tibia with scattered row of 15–20 stout spines on anterior edge; hind coxa with distinct basolateral tubercle. **Wings** (Fig. 2): fore wing vein r nearly as long as 3RSa, vein m-cu interstitial with 2RS, first subdiscal cell open, vein 2cu-a absent; hind wing vein M+CU about equal in length to 1M, vein m-cu curved slightly toward wing apex. **Metasoma** (Fig. 6): first tergum longitudinally costate-rugulose, wider at apex than long, medially with two strong longitudinal carinae setting off raised median area and



Figs. 1-2. Wings of *Allorhogas* species. 1, *brasiliensis* n. sp. 2, *spermaphagus* n. sp.

connected at base by distinct cross carina; tergum 2+3 longitudinally costate on basal 2/3, remainder coriaceous, groove between terga 2 and 3 weak or absent; tergum 4 costate on basal 1/5, remainder coriaceous; remainder of terga coriaceous; ovipositor about 2/3 length of metasoma.

Male.—Essentially as in female; femora swollen, hind femur with length about twice width.

Holotype Female.—BRASIL: Poço das Antas Biological Reserve, Silva Jardim County, Rio de Janeiro State, September 1995, M. V. Macêdo, reared from seeds of *Stryphnodendron* sp. Deposited in Depar-

tamento de Ecologia-IB-CCS, Universidade Federal do Rio de Janeiro, Brasil.

Paratypes.—BRASIL: 7 females, 4 males, same data as holotype. Deposited in: Universidade Federal do Rio de Janeiro, Brasil; Universidade Federal de São Carlos, Brasil; National Museum of Natural History, Washington, DC.

Comments.—This species is very similar to *brasiliensis*, but the most consistent distinguishing characters are: smaller size (3.5–3.75 mm) than in *brasiliensis* (4.0–4.5); antenna with 29–30 antennomeres (34–35 in *brasiliensis*); entirely brown flagellum (yellow at base, brown at apex in *brasiliensis*).



Figs. 3–6. *Allorhogas spermaphagus* n. sp. 3, vertex. 4, mesosoma, lateral view. 5, mesosoma, dorsal view. 6, metasoma, dorsal view.

sis); fore wing vein m-cu interstitial with vein 2RS (basad of 2RS in *brasiliensis*); fore wing vein r about equal to vein 3RSa (3/4 length of 3RSa in *brasiliensis*). In some specimens of *spermaphagus* the face is often more distinctly rugose near the eyes than in *spermaphagus*; also the vertex of *spermaphagus* is often rugulose behind the ocelli but usually only coriaceous in *brasiliensis*.

Biology.—This species was reared from seeds of *Stryphnodendron polyphyllum* Martius (Leguminosae) which is native to the Atlantic forest region of Brasil. The biology

is similar to that described for *A. dyspistus* by Macêdo and Monteiro (1989) and Macêdo et al. (1998). Pods of *Stryphnodendron* contain about 10 seeds arranged side by side. The *Allorhogas* female oviposits directly into immature seeds when abundant endosperm and a small embryo are still present. Oviposition is directly through the pod wall and the egg is placed inside the seed. After oviposition by the braconid, the seed divides internally and externally (see Macêdo et al. (1998)), resulting in an intact region joined to the funicle where the seed embryo is

usually found. In many cases this region of the seed continues growing even after the adult *Allorhogas* has emerged. In most of the attacked seeds that were observed ($n = 34$) more than one *Allorhogas* was found in a single seed—29% were observed to have two braconids per seed and 62% had three per seed. In these cases, more than one division of the seed occurs but a single intact region is still found with the seed embryo.

Two species of chalcid wasps were reared from the same pods: *Lycrus* sp. (Pteromalidae) and *Eurytoma* sp. (Eurytomidae). Although we did not observe these wasps emerging directly from *Allorhogas* larvae, one was observed feeding on an *Allorhogas* larva. Because the chalcid pupae were dissected from seeds exhibiting the same damage caused by the braconids, we are assuming the chalcids were attacking the *Allorhogas*.

Etymology.—The specific name is from the Greek *sperma* meaning seed and the Greek *phagein* meaning to eat in reference to the biology of this seed-eating braconid.

Allorhogas brasiliensis Marsh, new
species
(Fig. 1)

Female.—**Body color**: head, mesosoma and metasoma dark honey yellow, propodeum and mesonotum often light brown; legs yellow; flagellum honey yellow on basal 1/2, turning to brown on apical 1/2; wings hyaline, fore wing vein C+Sc+R yellow, stigma brown, rest of veins light brown, hind wing veins yellow. **Body length**: 4.0–4.5 mm. **Head**: 34–35 antennomeres; face rugulose-coriaceous; frons excavated, coriaceous; vertex and temple coriaceous; malar space 1/3 eye height; oral opening small, circular, diameter equal to basal width of mandible; ocell-ocular distance twice diameter of lateral ocellus; occipital carina distinct, meeting hypostomal carina. **Mesosoma**: pronotum weakly rugulose-coriaceous laterally with deep median scrobiculate

groove bordered ventrally by carina; mesonotum sharply declivous anteriorly, mesonotum and scutellum coriaceous, middle lobe with median scrobiculate groove not extending to anterior edge of mesonotum; notauli distinctly scrobiculate, meeting in large rugose area before scutellum; scutellar furrow with three cross carinae; mesopleuron coriaceous, sternaulus deep, scrobiculate; propodeum rugose, with two baso-lateral semicircular rugulose-coriaceous areas enclosed by carina, apical area above metasoma insertion strongly rugose. **Legs**: fore tibia with scattered row of 15–20 stout spines on anterior edge; hind coxa with distinct baso-lateral tubercle. **Wings** (Fig. 1): fore wing vein r about 3/4 length of 3RSa, vein m-cu meeting RS+Ma slightly before 2RS, thus a short segment of (RS+M)b visible, first subdiscal cell open, vein 2cu-a absent; hind wing vein M+CU about 3/4 length of 1M, vein m-cu curved slightly toward wing apex. **Metasoma**: first tergum longitudinally costate, wider at apex than long, medially with two strong longitudinal carinae setting off raised median area and connected at base by distinct cross carina; tergum 2+3 longitudinally costate on basal 2/3, remainder coriaceous, groove between terga 2 and 3 weak or absent; tergum 4 costate on basal 1/5, remainder coriaceous; remainder of terga coriaceous; ovipositor slightly more than 1/2 length of metasoma.

Male.—Essentially as in female; femora swollen, hind femur with length about twice width; propodeum and first metasomal tergum dark brown.

Holotype Female.—BRASIL: Poço das Antas Biological Reserve, Silva Jardim County, Rio de Janeiro State, October 1995, M. C. Pimentel, reared from seeds of *Pithecellobium* sp. Deposited in Departamento de Ecologia-IB-CCS, Universidad Federal do Rio de Janeiro, Brasil.

Paratypes.—BRASIL: 6 females, 6 males, same data as holotype. Deposited in Universidade Federal do Rio de Janeiro, Brasil,

Universidade Federal de São Carlos, Brasil, and National Museum of Natural History, Washington, DC.

Comments.—See comments under *spermaphagus* for distinguishing characters of the two species.

Biology.—This species was reared from seeds of *Pithecellobium pedicellare* (DC.) Benth. Preliminary observations show that the biology is similar to that of *A. spermaphagus*. The seed damage caused by both *A. spermaphagus* and *A. brasiliensis* is very similar to that observed for *A. dyspistus*.

Etymology.—The specific name is in reference to the locality of this species.

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Description of a New Species of *Emersonella* (Hymenoptera: Eulophidae) from Brazil, with Preliminary Observations on its Biology

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Abstract.—*Emersonella trimaculata* Azevedo and Silva, new species, an egg parasitoid of chrysomelids, from northeastern Brazil is described and illustrated. Host age influences percent parasitism, which decreases as age increases, but it does not influence the sex ratio. The egg phase has an average duration of 1.05 ± 0.04 days, larval phase of 5.04 ± 0.19 days, pupal phase of 6.74 ± 1.16 days. The total time of development is 13.29 ± 0.53 days for males and 13.96 ± 0.48 days for females.

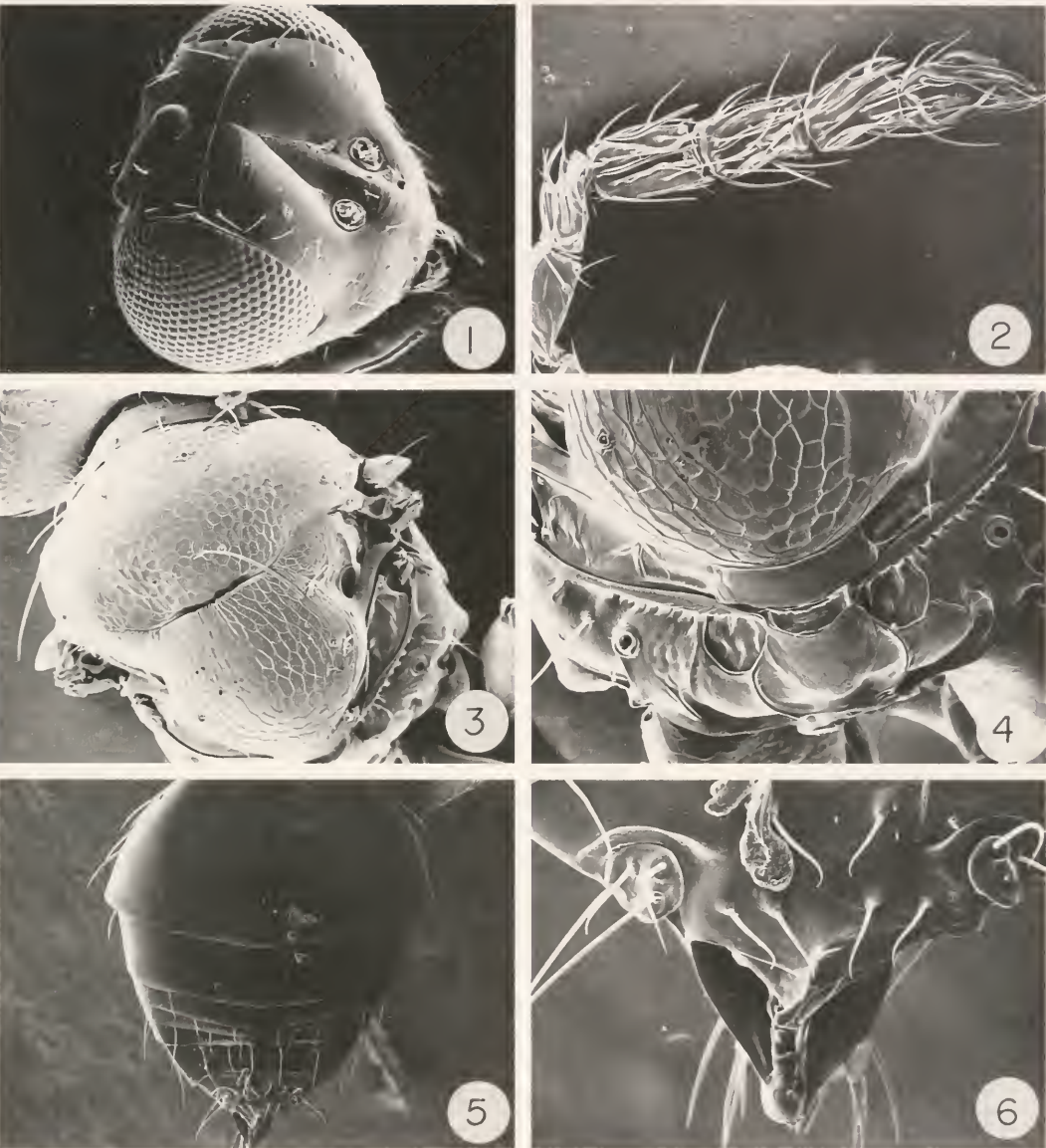
Emersonella Girault is a small genus of Entedoninae (Hymenoptera, Eulophidae) restricted to the New World (Boucek 1977). All species with known biology are idiobiont endoparasitoids of eggs of Chrysomelidae (Cox 1994), mainly Cassidinae. De Santis (1983) revised the genus and described four species from Brazil, Argentina and Uruguay. In this paper, a new species of *Emersonella* from the State of Maranhão in northeastern Brazil, is described and illustrated. Some preliminary biological studies are also included. Influence of the host age on the capacity of parasitism and sex ratio of the parasitoid is verified, the egg morphology is characterized, and the longevity of the egg, larval and pupal phases are determined.

MATERIAL AND METHODS

Morphological terminology for the description generally follows Gibson (1997) and sculpture follows Harris (1979). The material examined was provided by the Entomological Collection of Universidade Federal do Espírito Santo (UFES) and Universidade Federal de Viçosa (UFVB).

For the biological studies, mated and nulliparous females were maintained separately in flasks of 50ml containing a drop of a 1:1 solution of honey and water stuck to the wall of the glass as food, covered with cotton and kept at $28 \pm 1^\circ\text{C}$. The parasitoid and its host *Zatrephina meticulosa* (Spaeth) (Coleoptera, Chrysomelidae) was obtained from field collections from São Luiz, State of Maranhão, northeastern Brazil. This beetle occurs naturally on the leaves of *Ipomoea pes-caprae* L. (Convolvulaceae) in coast sand plain.

Two experiments were carried out. Experiment 1 was to verify the influence of the host age on the percent parasitism and sex ratio of the parasitoid. In this experiment, 80 egg masses of *Z. meticulosa* of different ages, varying from 1 to 8 days, were offered to females, separately in a flask. The females were kept with the host egg masses for 10 days before being removed from the flasks. Experiment 2 was to verify the duration of the egg, larval and pupal phases, and morphological characteristics of the egg. Host egg masses at 48



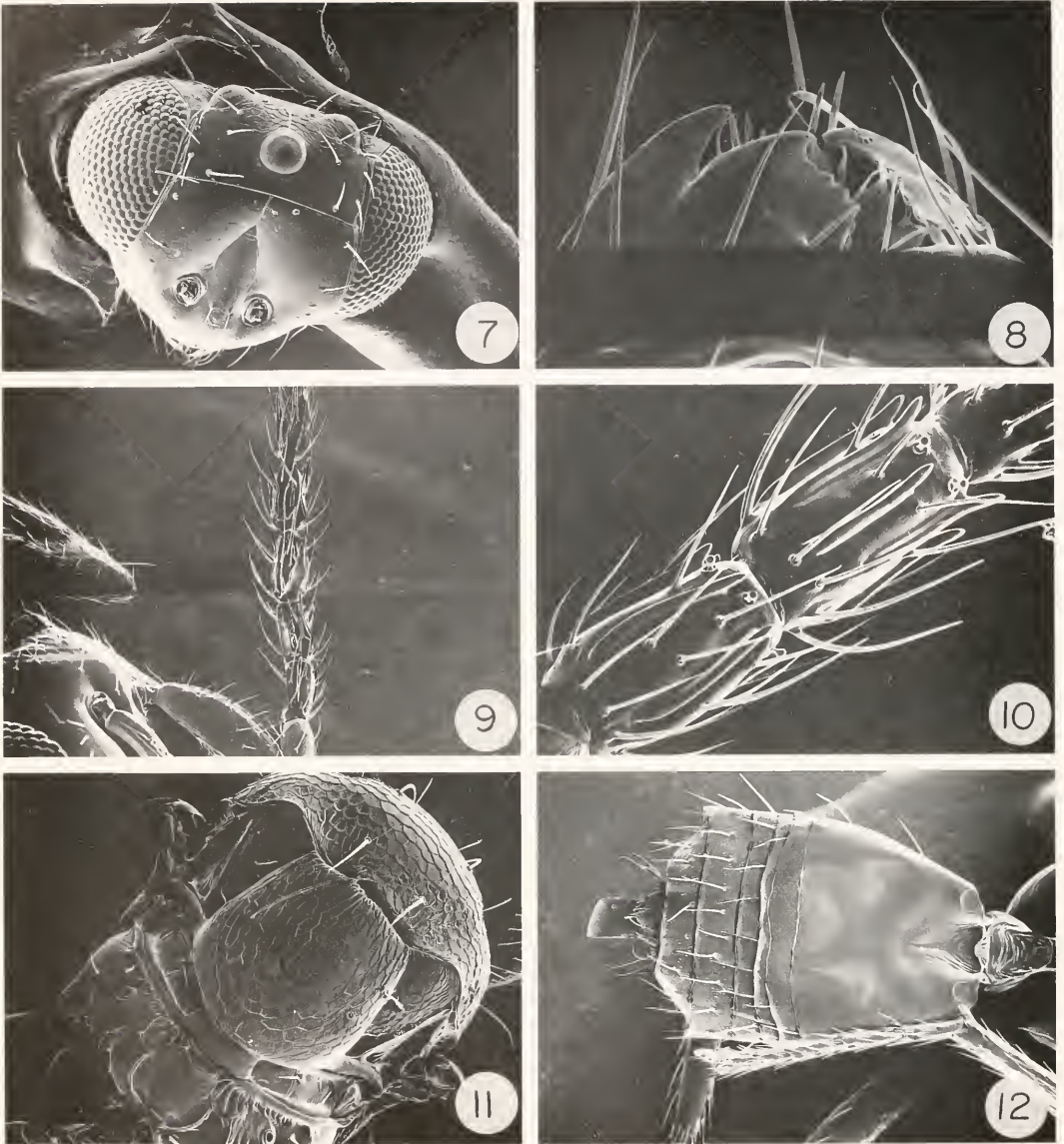
Figures 1–6. *Emersonella trimaculata*, female, dorsal view. 1, head; 2, antenna; 3, thorax; 4, propodeal disc; 5, metasoma; 6, ovipositor sheathes.

hours old were offered to groups of 30 to 40 nulliparous, recently mated females for 3 hours. To verify the phase of parasitoid development, samples of 15 host eggs were dissected in physiologic solution, at intervals of 24 hours. To verify the parasitoid egg phase, 10 host eggs were observed at one hour intervals. Observations were made from the 15th until the 29th hour

to determine the type, morphology and size of the egg.

Emersonella trimaculata Azevedo and
Silva, new species
(Figs. 1–12)

Female.—Length 0.85–1.01mm. Head and body black, except: head, scutellum and propodeum with yellowish green me-



Figures 7–12. *Emersonella trimaculata*, male, 7, head, dorsal view; 8, mandibles, lateral view; 9, antenna, lateral view; 10, antenna sensillae, lateral view; mesosoma, dorsal view; 12, metasoma, dorsal view.

tallic reflections; pronotum and scutum with blue metallic reflections; mandible testaceous-brown; scape yellowish white, pedicel brown, flagellomeres black; legs slightly yellowish, distal tarsomeres and anterior face of fore femur darker, coxae black with weak blue metallic reflection; bristles on body pale yellow; wings hyaline and veins light brown. **Head** (Fig. 1):

1.22–1.42 X as wide as long, 1.06–1.18 X wider than thorax in dorsal view. Frons and gena smooth, face nearly so, vertex imbricate. Distance between lateral ocelli 2.25–3.0 X as long as distance from lateral ocelli to eye. Transverse fronto-facial suture complete and conspicuous. Scrobal depression as long as scape. Malar space about 0.43–0.53 X the height of eye. To-

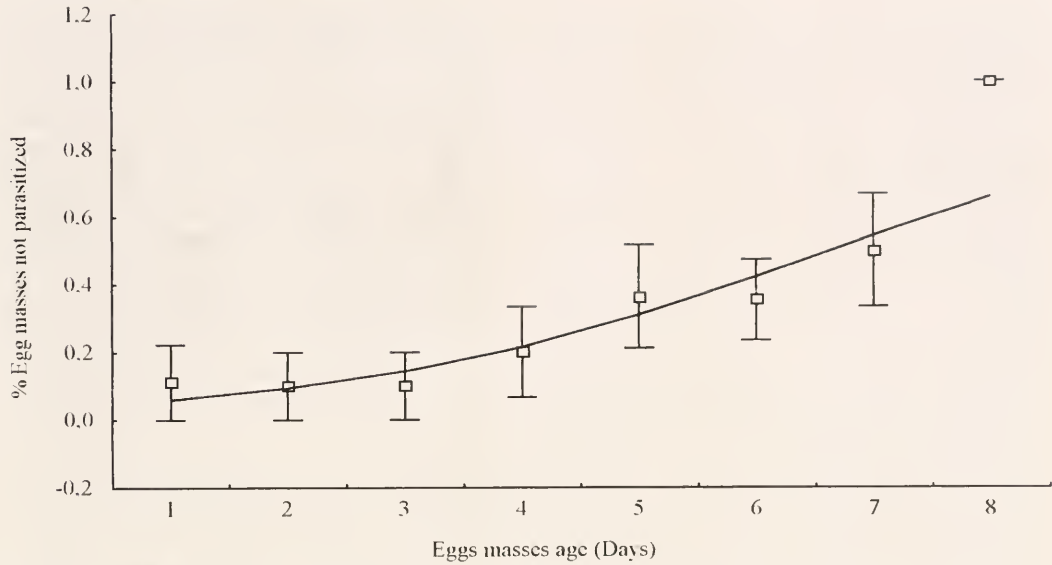


Figure 13. Percentage of egg mass posture not parasitized by *Emersonella trimaculata*, in different ages of the host eggs. The bars represent the standard deviation.

rulus slightly closer to eye margin than clypeus. Vertex with ocular-ocellar suture. Eye with short hairs. Mandible bidentate, the lower larger, and the upper with upper margin serrated (Fig. 8). Antenna (Fig. 2): scape 3.75–4.3 X longer than wide; pedicel almost twice as long as wide; three anelli, the first slightly larger, the others subequal, funicular segments subquadrate, slightly longer than wide, club unisegmented, apex extended into terminal spine, 2–3 X longer than wide and 1.33–1.5 X longer than funicular segments. Sensillae capitate and elongate with apex slightly directed upward (Fig. 10). **Mesosoma** (Figs. 3–4): subquadrate in dorsal view, 1.16–1.25 X longer than wide, arched in lateral view. Pronotum not visible in full dorsal view, with a row of six setae along the posterior margin. Mesoscutum foveolate, with two rows of two adnotaular setae on each side, notaulus very weak, missing medially. Scutellum imbricate, enlarged, 0.75–0.89 X longer than mesosoma, 0.55–0.58 X as wide as mesosoma, about as long as wide, lateral sides distinctly convex. Dorsellum smooth.

Propodeum smooth, with a pair of subtriangular depressions touching the anterior margin, with weak longitudinal striae medially, separated from each other by 1.2–1.5 X their width, without median carina and plica, with a sublateral carinae strongly arched, spiracle rounded, separated from the anterior margin of propodeum by about 1.0 X their diameter. Callosus with two setae. Mesopleuron with a small anterior central pit. Forewing with marginal vein 2.3–2.4 X longer than submarginal vein. Postmarginal vein about as long as stigmal vein. **Metasoma** (Fig. 5): stout, subsessile, with few setae, 1.03 X as long as mesosoma; first gastral tergite large, about 0.5 X length of gaster, lateral margin evenly convex in dorsal view. Ovipositor sheath short (Fig. 6), anterior half concealed, ovipositor stylus 0.87 X as long as gaster.

Male.—Length 0.9–1.06 mm. Same color as female, except by: fore femur, fore tarsus and the other distal tarsomeres darker; gaster with three yellowish white spots, a pair of spots at anterior corner of first gastral segment, straight anteriorly and

rounded behind, separated from each other by 2.2–2.5 X their diameter, the third spot very large, occupying nearly the entire width of the posterior half of the first gastral tergite. **Head** (Fig. 7): Distance between lateral ocelli about 4–6 X as long as distance from lateral ocellus to eye. Antenna (Fig. 9): funicular segments slender, in ratio of about 2:2.2:6:2.3 X as long as wide; club 3–4 X as long as wide. **Mesosoma** (Fig. 11): 1.29–1.66 X longer than wide, scutellum 0.6–0.66 X wider than mesosoma. Forewing with marginal vein 2.1–2.4 X longer than submarginal vein. **Metasoma** (Fig. 12): petiolate, petiole larger behind, first gastral tergite 1.4–2 X longer than the rest of gaster, with anterior margin straight medially and angulate at corner laterally. Genitalia: paramere developed inward ventrally, with an apical setae directed outward; digitus wide, with two conspicuous spines directed outward apically, and with a small outer tooth; aedeagus with two lobes rounded apically; phallobase little developed in ventral side; aedeagus apodeme extending beyond the basal margin of phallobase only slightly.

Material examined.—♀ holotype, 11 ♀♀ and 15 ♂♂ paratypes BRAZIL, Maranhão, São Luiz, coast sand plain vegetation, 26.i.1998, J. C. Silva Jr. col. (UFES); 298 ♀♀ and 298 ♂♂ BRAZIL, reared in laboratory (AMNH, BMNH, CASC, CNCI, CUIC, DCBU, DZUP, EMUS, FSAC, IGBE, INPA, LACM, MCZH, MEPC, MZSP, OSUC, PMAE, UCDC, UCRC, UFES, UFVB, USNM).

Remarks.—This species runs to *Emersonella niveipes* Girault in the key presented by De Santis (1983), but here the mandible is bidentate and the male has three white spots in the gaster, while *E. niveipes* has the mandible with six teeth and the male has two transverse stripes just beyond the middle of the gaster. *E. ooeica* De Santis and *E. lecitophaga* De Santis are two species with a sub-basal white spot in the gaster of males as in *E. trimaculata*, but here there are two additional small spots in

front of the large one, and the femora and tibiae are yellowish white rather than black as in the two former species. This species is also similar to *E. rotunda* (Ashmead), but in the last species the mid and hindcoxae are white and funicular segments are slightly longer. *Emersonella trimaculata* displays the same pattern of sexual dimorphism as other species in the genus. The male has funicular segments longer than those of the female and the gaster has three light spots on the first gastral tergite, while in the female the gaster is evenly black.

Biology.—A total of 80 egg masses were analyzed, with 57 parasitized (71.3%) and 23 (28.7%) not parasitized. The results indicate that host age influences parasitism by *E. trimaculata*. Parasitism decreased when older egg masses were offered to the females (logistic regression $\chi^2 = 12.7$; g.l. = 1 and $p < 0.01$; Fig. 13). The variation observed in parasitism was from only 11% not parasitized in the one-day-old egg masses up to 100% not parasitized in the eight-day-old egg masses.

According to the logistic regression, the expected value for eight-day-old egg masses was approximately 65% not parasitized, although the value was 100%. Only three egg masses were observed in the samples on the 8th day, while for the other days the number of egg masses was never smaller than nine. This difference might explain the deviation in relation to the model.

This same pattern was observed when the number of individual eggs parasitized was verified in each egg mass. Parasitism varied on the average from 81%, for one-day-old egg masses, up to 12%, for eight-day-old egg masses. Thus, as age of host increases, a reduction in parasitism occurs in both the number of egg masses and the number of eggs parasitized with each mass.

Host age does not influence sex ratio. The difference in sex ratio produced by females of *E. trimaculata* in egg masses of

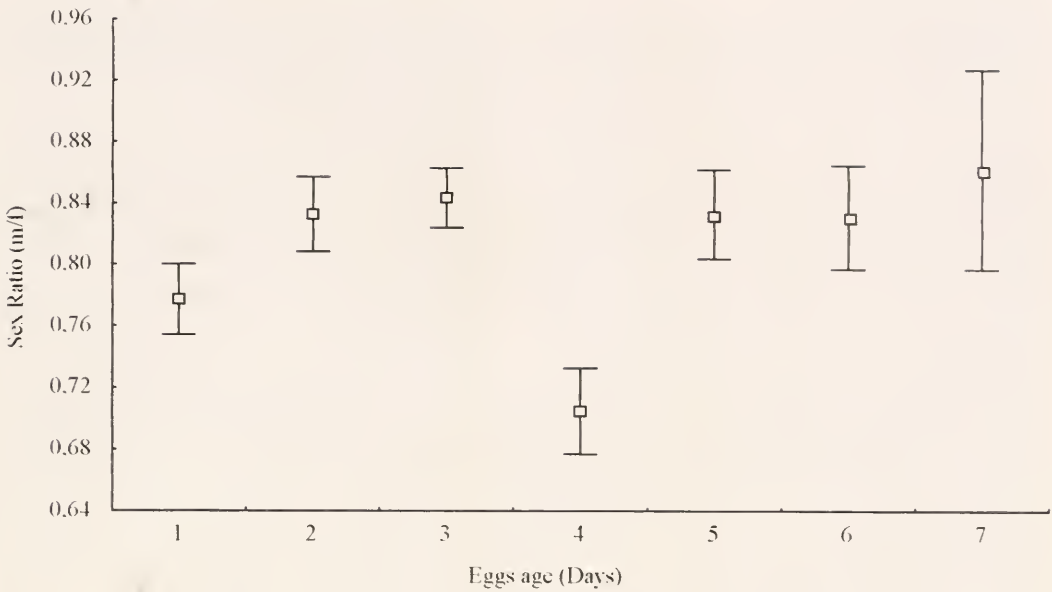


Figure 14. Relationship between the age of the egg and the sex ratio of *Emersonella trimaculata*. The bars represent the standard deviation.

different ages is not significant ($\chi^2 = 0.2$; g.l. = 1 and $p = 0.7$; Fig. 14).

E. trimaculata eggs are $25.6 \pm 1.4 \mu\text{m}$ in length with a maximum width of $6.8 \pm 1.0 \mu\text{m}$ (Fig. 15). The eggs are simple, hymenopteriform, oblong or ovoid, slightly arched and with both poles smoothly round, with chorion delicate and without ornamentation as usually found in Hymenoptera (Clausen 1940). The egg phase had an average duration of 1.04 ± 0.04 days. The micropyle of the eggs was not observed, probably due to the transparency of the eggs (Fig. 15). However, there

is a differentiated area in the anterior area, which might indicate the presence of the micropyle, which is usually located in the anterior region of the egg. In some species, however, it has been observed in the posterior area (Quicke 1997).

The larval phase has a duration of 5.0 ± 0.2 days, while the pupal phase lasts 6.7 ± 1.2 days. The pigmentation process begins in the first day of the pupal phase. Males of this species emerge before the females ($\chi^2 = 99.13$; $p < 0.01$), with almost all males emerging by the end of the sixth day of the pupal stage (91.56%), but only

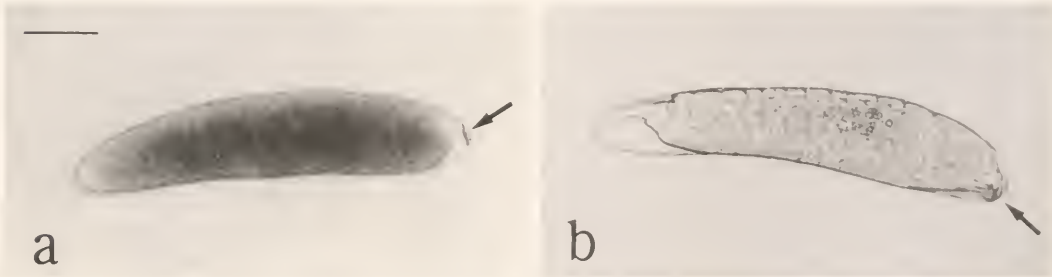


Figure 15. Eggs of *Emersonella trimaculata*; a, 2 hours of development; b, 20 hours of development. (Scale bar = $5 \mu\text{m}$).

65.47% of the females. The total time of development was 13.3 ± 0.5 for males and 14.0 ± 0.5 for females.

In *E. trimaculata*, a small variation is seen in the duration of the egg and larval phases and a larger variation in the pupal phase. This can indicate the existence of mechanisms that synchronize the phases in this species. The results seem to indicate an abbreviation of the pupal phase of the males without loss of absorption of nutrients, since size differences do not exist between males and females.

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***Trisecodes* gen. n., (Hymenoptera: Eulophidae: Entedoninae), the First Eulophid with Three Tarsal Segments**

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Abstract.—The neotropical genus *Trisecodes*, and its type species *T. agromyzae*, are described in the eulophid subfamily Entedoninae. Its placement within the Chalcidoidea and the Eulophidae is discussed. Its hosts, all belonging to Agromyzidae (Diptera) are listed. This is the first Eulophidae, as well as the first member of the Chalcidoidea outside of the Trichogrammatidae, where both sexes have three tarsal segments.

Résumé. Les auteurs décrivent le nouveau genre néotropical *Trisecodes*, ainsi que son espèce type, *T. agromyzae*, dans la sous-famille des Entedoninae (Eulophidae). Ils discutent ensuite de sa position systématique à l'intérieur des Chalcidoidea puis des Eulophidae. Ils citent les hôtes de cette espèce, qui appartiennent tous à la famille des Agromyzidae (Diptera). Il s'agit du premier Eulophidae, mais aussi du premier chalcidien n'appartenant pas aux Trichogrammatidae, dont les deux sexes présentent des tarses trimères.

Understanding the evolution of the superfamily Chalcidoidea, and deriving robust phylogenetic hypotheses, is a major challenge. The difficulty comes from the biodiversity of the group, one of the most speciose superfamilies of the Hymenoptera (Noyes 1998), and the plasticity of both morphological and biological features exhibited by these wasps (Gibson 1990; Gibson *et al.* 1999). The genus described below is an example of such plasticity. Up to now, the only Hymenoptera known to have 3-segmented tarsi were members of the family Trichogrammatidae, and some highly derived and dimorphic male fig wasps (Agaonidae). The presence of three tarsal segments in both sexes has been considered a synapomorphy for the Trichogrammatidae, many of whose members also have lines of setae on the forewing. The wasp described in this paper, *Trisecodes agromyzae*, shares these features with the Trichogrammatidae but does not belong to this family.

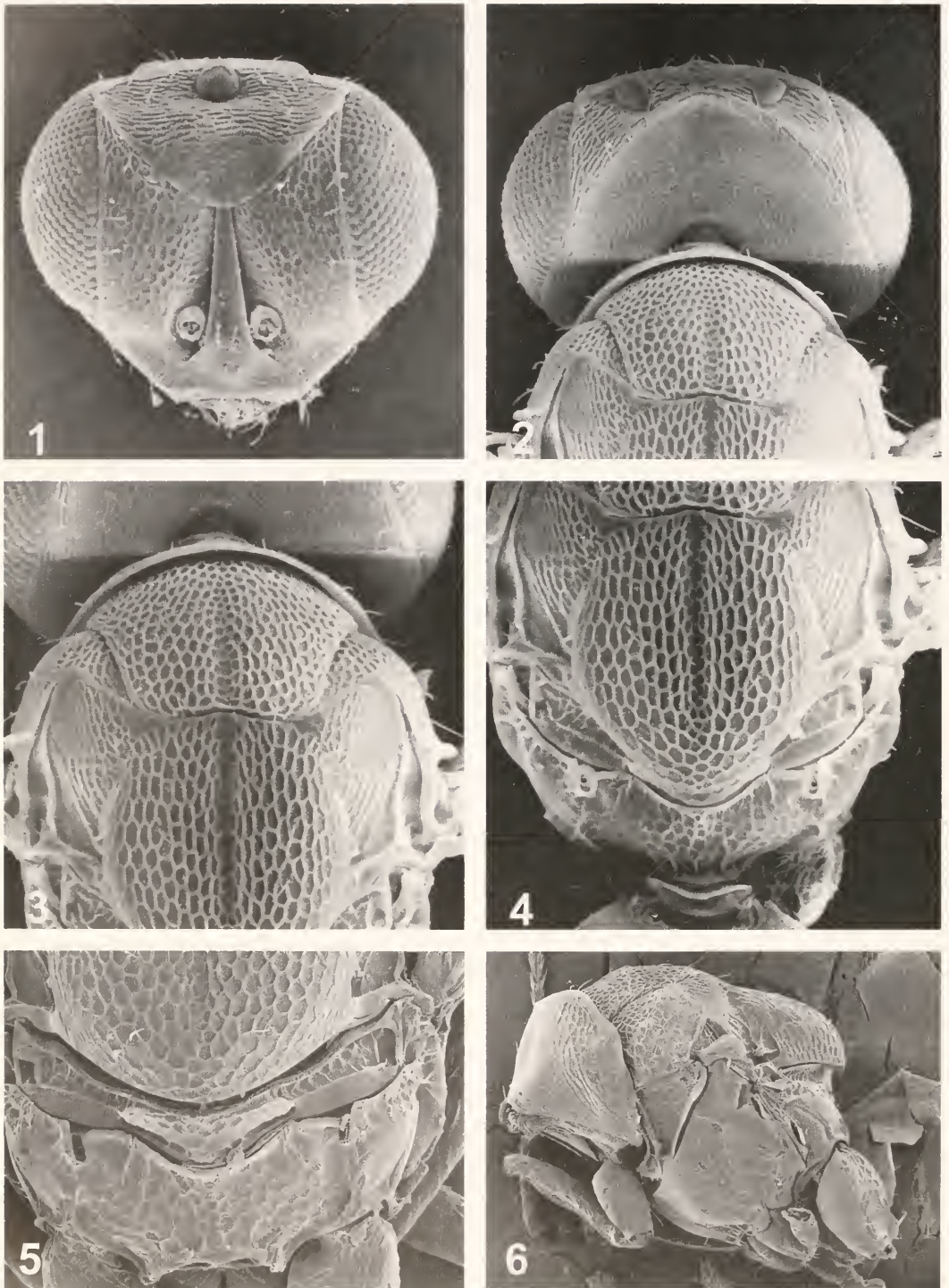
Specimens of the newly described species have been deposited in the following institutions: Natural History Museum, London, UK (BMNH), Centre de Coopération Internationale en Recherche Agronomique pour le Développement, Montpellier, France (CIRAD), United States National Museum, Washington D. C., USA (USNM), Canadian National Collection of Insects and other Arthropods, Ottawa, Canada (CNC).

***Trisecodes* Delvare and LaSalle, new genus (Figs. 1–12)**

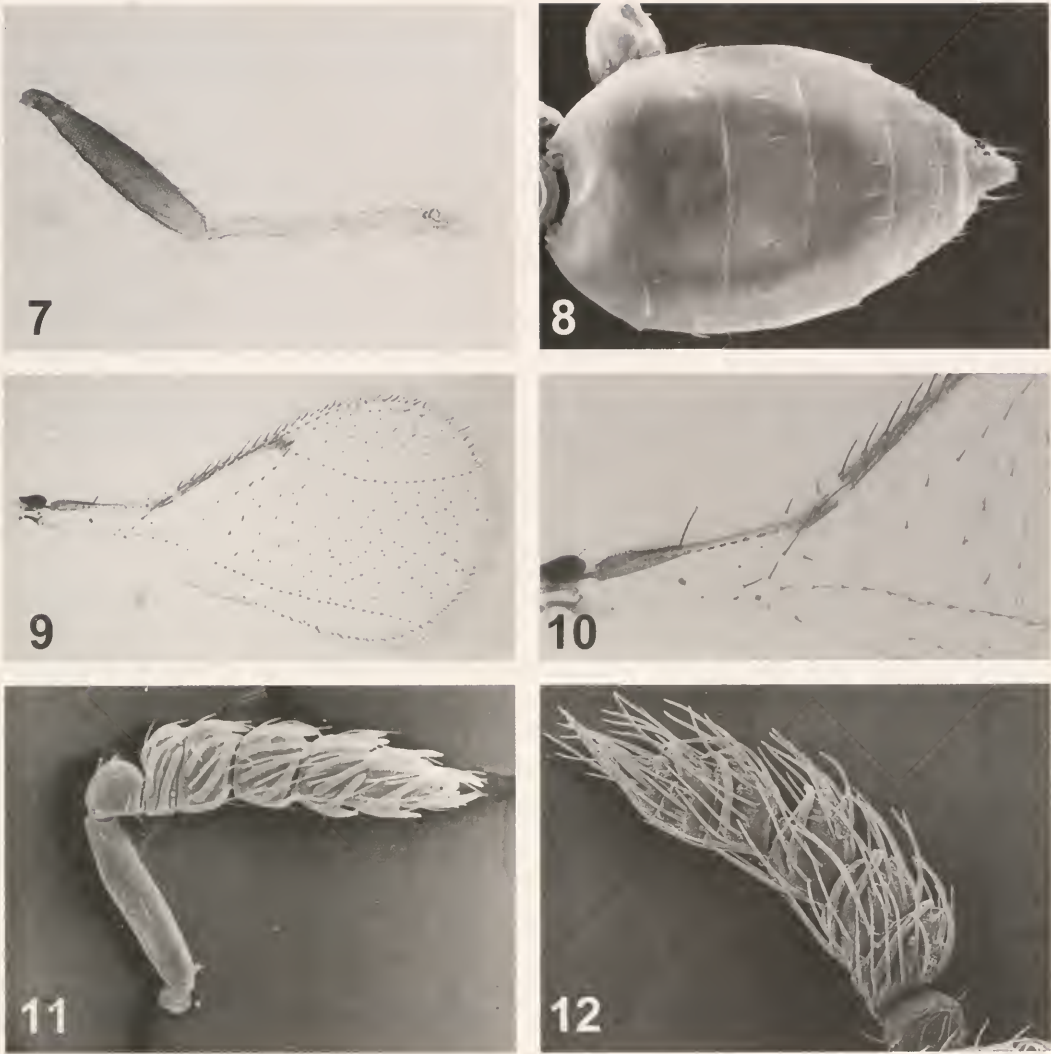
Name derivation.—A combination of *tri*-suggesting the tarsal formula and *-secodes* from *Asecodes*, a genus of Entedoninae. Some members of *Asecodes* have lines of setae on the forewing which are similar to those seen in *Trisecodes*. Gender neuter.

Type species.—*Trisecodes agromyzae* Delvare and LaSalle, new species.

Head (Fig. 1): Frons with distinct scrobal



Figs. 1-6. *Trisecodes agromyzae*, new genus, new species. 1, head in frontal view; 2, head and basal part of mesosoma in dorsal view; 3, mesonotum; 4, apical part of mesosoma; 5, propodeum in posterior view; 6, mesosoma in lateral view.



Figs. 7–12. *Trisecodes agromyzae*. 7, fore tibia and tarsus; 8, female metasoma in dorsal view; 9, forewing; 10, detail of the base of the forewing; 11, female antenna; 12, male flagellum.

sutures which extend dorsally to the frontal sutures and define a median strip, the strip slightly raised over the surface of the frons and slightly overlapping it laterally. Frontal sutures V-shaped, clearly separated from the median ocellus. Malar sulcus groove like. Clypeus not delimited from lower face. Mandibles bidentate, the teeth acute, of same length. Maxillary palpi bisegmented, labial palpi unisegmented. Labrum strongly bilobed ventrally. **Antenna** (Figs. 11–12): Flagellum with one anellus,

a 3-segmented funicle and a 3-segmented clava. Funicular segments transverse, bearing multiporous plate sensilla of two types: usual ones, as found in other Chalcidoidea (elongate sensilla longitudinally oriented with raised and sharp apex) and half-ring ones, embracing each of the segments as well as the apex of the clava; latter sensilla are in oblique or even transverse orientation (except on third claval segment). Multiporous plate sensilla of the usual type are replaced in males by

whorls of long setae. **Mesosoma** (Figs. 2–6): Pronotum and mesonotum with distinct raised reticulation, same short and very sparse setae, the former narrowly visible dorsally, with its posterior margin deeply emarginate. Mesoscutum and scutellum with distinct median furrow. Notauli complete, straight, of same appearance throughout. Axillae distinctly protruding anteriorly. Scutellum without sub-lateral furrows or lines, distinctly convex both dorsally and laterally. Propodeum mostly reticulate, with spiracular groove hardly impressed, without subspiracular tubercle, supracoxal flange and nucha. Spiracle formed through incision of the anterior margin of the propodeum, not completely closed. Phragma not reaching the posterior margin of the mesosoma. Prepectus large, reticulate, triangular in lateral view. Mesopleuron convex anteriorly, femoral scrobe reticulate, upper mesepimeron very large, separated from lower mesepimeron by a row of punctures, the latter very small. Metapleuron small but visible, triangular, delimited from the propodeum by a broad, shallow groove. **Legs** (Fig. 7): All tarsi 3-segmented, segments about of same length. Apical spur of foretibia slightly curved, bifid, the furca at mid length of the spur, the inner branch hardly visible and much shorter than the outer one. **Wings** (Figs 9–10). Submarginal vein with one dorsal seta. No break between submarginal vein and parastigma, but a hyaline break between parastigma and marginal vein. Forewing with stigmal and postmarginal veins very short. Disc of wing sparsely setose. Hairlines (Rs1 and r-m) originating from stigmal vein present. Cubital vein setose and distinct. **Metasoma** (Fig. 8): Gaster on a transverse petiole, with 7 tergites. Last tergite not subdivided. Cercal hairs on small tubercles.

Trisecodes agromyzae Delvare and
LaSalle, new species
(Figs. 1–12)

Female.—Length 0.70–0.85 mm. **Color**: Body, legs except tarsi and antennae dark

with slight bluish reflections. Tarsi whitish. Wings hyaline. Veins dark brown. **Head** (Fig. 1): Relative measurements (made from a slide mounted specimen): Height 70, width 87, fronto-vertex in front of the median ocellus 48, POL 23, OOL 9, lateral ocelli diameter 7, eyes height 43, width of eye (frontal view) 16, malar space 20, oral fossa 21, antennal toruli-eye distance 14, distance between toruli 10, toruli diameter 7, toruli-lower margin of clypeus length 10. Inner margin of eyes parallel. Malar groove nearly straight as well as genae. Labrum with a row of 4 hairs (one specimen examined). Lower edge of antennal toruli at lower eye margin. One row of 7–8 hairs along inner margin of eye plus one pore. Lower face very faintly squamose, frons reticulate. Upper frons, above frontal sutures, coriaceous (= engraved reticulate), more or less imbricate, vertex with elongate cells which are transversely oriented on its anterior part then oblique. **Antenna** (Fig. 11): Scape nearly 5 times as long as wide (28:6). Pedicel slightly longer than wide (in lateral view 9:7). First funicular segment very transverse (7:11), following segments progressively less so. First claval segment slightly transverse (10:12), second one subquadrate, last one elongate (9:5). Each of the flagellar segments bearing 3 ring-like sensilla, in nearly transverse orientation on F1, more oblique in the following segments. Two elongate sensilla at apex of M3 are pincer-like. **Mesosoma** (Figs. 2–6): Relative measurements: Length 95, width 66, length of mesoscutum 37, of scutellum 45, width of latter 40. Pronotum bearing 3–4 pairs of setae on posterior margin. Mid lobe of mesoscutum bearing 7–8 pairs of short setae laterally. Median furrow on posterior two thirds, smooth on bottom. Scutellum with furrow visible on anterior four fifths. Three pairs of short hairs respectively slightly before and behind mid length of scutellum, last pair, longer, near apex. Dorsellum as a raised reticulate plate. Lateral part of metanotum also reticulate but

sculpturing finer than on dorsellum. Propodeal callus with one short seta. Lower mesepimeron ventrally punctate. Metapleuron smooth. Fore basitarsus with a row of 5 bristly hairs ventrally. Relative measurements on mid leg. Tibia 51, tarsus 40, basitarsus 15 (on dorsal outline), apical spur of tibia 14; latter simple and straight. Measurements of hind leg. Tibia 53, basitarsus 14, apical spur of tibia 7. **Forewing** (Figs 9–10): Relative measurements: Length 164, width 82, costal cell 45, marginal vein 40, stigmal 5, postmarginal 3, fringe 9. Wing very distinctly widened at apex and regularly rounded. Costal cell with 3–4 dorsal hairs at apex, ventrally bare. Parastigma bearing 2 dorsal hairs, marginal vein with 9–10 dorsal hairs of about twice the width of the vein. A line of 7–8 setae present near anterior wing margin, originating near stigmal vein and extending apically. Basal vein with 2–3 hairs; another one closely beside it. Anal vein (subcubital) represented by a row of 5–6 sparse hairs in front of the retinaculum and more basally by 2–3 isolated hairs behind the basal vein. Basal cell bare. **Hind wing**: Relative measurements: Length 112, width 33. Wing bearing 3 hamuli, narrowly rounded at apex. **Metasoma** (Fig. 8): petiole with transverse lamina on anterior margin. Gaster about 1.35 times as long as wide (95:69) on slide-mounted specimens. Gastral tergite 1 depressed behind petiole. Tergite 2 with a row of 5 hairs laterally (Fig. 8). Each of the following tergites with one dorsal line of hairs. Ovipositor valvula 70, gonostyli 12. Anterior end of the ovipositor near the base of the gaster. Cercal hairs short, on small tubercles.

Male (Fig. 12).—Length 0.60–0.80 mm. All characters identical but antennal flagellum devoid of elongate sensilla, latter replaced by whorls of long hairs. Only 1, rarely 2, ring-like sensilla on each of the flagellar segments. Gaster length 80, width 45. One long cercal hair. Two long hairs on apex of epipygium.

Material examined.—Holotype ♀: BELIZE: Cayo Province, Las Cuevas, 550 m, Chiquibul Forest (Lewis O. T.), ex *Haplomyza* sp. on *Senna cobanensis*, 27 VIII 1998 (N^o 5649) (Lewis O. T.) (in BMNH). Paratypes (in BMNH, CIRAD, USNM, CNC). Same locality and collector, ex *Calycomyza? cassiae* on *Senna cobanensis*, 21 IX 1997 (1 ♂, 4 ♀♀) (N^o 16.040, 16.042, 16.043 & 16.046), 26 IX 1997 (1 ♀) (N^o 389), 5 XI 1997 (1 ♂) (N^o 1543), 26 VIII 1998 (1 ♂, 1 ♀) (N^o 5573), 29 VIII 1998 (1 ♀) (N^o 5716) and 31 VIII 1998 (1 ♀) (N^o 5914), 4 IX 1998 (1 ♀) (N^o 6023); 1 ♂, same locality and collector, 5 II 1998 (N^o 1719); same locality and collector, on *Stizophyllum riparium*, 6 VI 1998 (1 ♂) (N^o 3300), 30 VII 1998 (1 ♂) (N^o 4895); 1 ♂, same locality and collector, ex *Nesomyza* sp. on *Amphilophium paniculatum* (N^o 4805); 1 ♂, same locality and collector, ex *Calycomyza* sp. on *Triumfetta bogotensis*, 6 VII 1998 (N^o 4305); 1 ♂, same locality and collector, on *Sida rhombilolia*, 11 VIII 1998 (N^o 5342); same locality and collector, ex *Calycomyza sidae* on *Sida acuta*, 10 X 1997 (1 ♂, 1 ♀) (N^o 905 & 598), 5 II 1998 (1 ♂, 4 ♀) (N^o 1700, 1701, 1702, 1703 & 1704); 5 IX 1998 (1 ♀) (N^o 6125). COSTA RICA: Guanacaste, Santa Rosa N. P., 300 m, 25 IV / 16 V 1987 (Janzen D. H. & Gauld I. D.) H-1-O (1 ♂) & H-2-C (1 ♂). GUADELOUPE: Bouillante, Pigeon, 7 XI 1995, reared from a leaf of *Daphnopsis americana* mined by *Liriomyza schmidtii* (Etienne J.) (1 ♀) (N^o 13783/GP 1195).

Distribution.—Belize, Costa Rica and Guadeloupe (Neotropical Region).

Hosts.—Agromyzidae (Diptera) mining plants belonging to various families (Bignoniaceae: *Stizophyllum riparium* and *Amphilophium paniculatum*; Leguminosae: *Sida rhombilolia*; Malvaceae: *Sida acuta* and *S. rhombifolia*; Thymeleaceae: *Daphnopsis americana*; Tiliaceae: *Triumfetta bogotensis*) and belonging to several different genera: *Liriomyza*, *Calycomyza* and *Nesomyza*.

According to O. T. Lewis (pers. comm.), *T. agromyzae* is a larval parasitoid.

Systematic placement.—The combination

of characters exhibited by *T. agromyzae* does not match any of the currently recognized families of chalcids. Trichogrammatidae is the only family of Hymenoptera having 3-segmented tarsi in both sexes, and it has long been considered to be one of the most easily recognizable and definable families of Chalcidoidea because of this character (Gibson *et al.* 1999). Additionally, many trichogrammatids have lines of setae on the forewing. On the surface, it would thus appear that *Trisecodes* should be placed in this family. However, the number of tarsal segments is a reduction character, and a loss of a tarsal segment (5 to 4) is seen many times in the Chalcidoidea in the families Eulophidae, Encyrtidae, Aphelinidae, Mymaridae, Tetracampidae, and even Pteromalidae (LaSalle *et al.* 1997). It is not inconceivable that the loss of an additional tarsal segment has occurred in one of these other lineages. The presence of lines of setae on the forewing radiating from the stigma is also known in several chalcid families: Trichogrammatidae, Eulophidae (Euderinae, Entedoninae), Torymidae and Pteromalidae (Colotrechninae, Ormocerinae: Systasini), and does not restrict a genus to any one family. Moreover, in trichogrammatids, the funicle is at most 2-segmented, the gaster is broadly attached to the mesosoma and the phragma goes into the metasoma, most often deeply so; the frontal sutures are also different from *Trisecodes*, the mesosoma never has raised reticulation, and the fore tibial spur is simple instead of bifid. Finally all the trichogrammatids whose biology is known are egg parasitoids of various insects.

Despite only having three tarsal segments, we are therefore placing *Trisecodes* in the Eulophidae. Unfortunately, there is little convincing morphological evidence for the monophyly of this family. The combination of 4 tarsal segments and a short, simple fore tibial spur have been considered to be the best characters supporting their monophyly, but LaSalle *et al.*

(1997) showed that the tibial spur is more variable than formerly thought. However recent molecular studies (Gauthier *et al.* 2000) demonstrate that Eulophidae when including *Elasmus* does actually represent a monophyletic group.

Many of the derived states found in *Trisecodes* are found in some eulophids (see Table 1). For example the shape and placement of the frontal sutures, the reduced number of tarsal segments, the reduced number of setae on the submarginal vein, the short stigmal vein, the very short post-marginal vein, and the presence of line of hairs on the forewing. The fore tibial spur of *Trisecodes* is also similar to what was recently illustrated for the Eulophidae (LaSalle *et al.* 1997). Eulophidae include finally many larval or/and pupal parasitoids of agromyzid flies.

If we consider the following suite of characters 1) reduced number in antennal segments; 2) special structure of the fore tibial spur; and 3) petiolate gaster with phragma restricted to mesosoma, not entering metasoma, then the unique possibility of familial placement for *Trisecodes* within a currently recognized family of Chalcidoidea is Eulophidae.

Table 1 lists the characters shared by *Trisecodes* with species of Eulophidae according to their subfamilial placement. Some are left unpolarized, others are derived. The table shows that *Trisecodes* shares the largest number of derived similarities with the Entedoninae.

It must however be mentioned that the placement of *Trisecodes* within this subfamily poses problems as it differs from most other entedonines in several important characters. Entedoninae is one of the best defined subfamilies of the Eulophidae (Boucek 1988; Schauff 1991). Support for its monophyly includes: scutellum with a single pair of setae; submarginal vein with two dorsal setae; mesoscutal midlobe with two pairs of setae; face with frontal sutures distinctly separated from the anterior ocellus; male scape with sensory pores

Table 1. Morphological characters of *Trisecodes* and their distribution in the subfamilies of Eulophidae.

Subfamily	Eulophinae	Euderinae	Tetrastichinae	Entedoninae
Character				
<i>Unpolarized characters</i>				
notauli:	many species	all species	all species	few species
complete and deep				
scutellum		all species		
general habitus				
mesonotum:	many species	most species	very few species	most species
raised reticulation				
mesopleuron				some species: (see Schauff 1991 fig. 81 p. 101)
<i>Derived states</i>				
antennal segments:	all species	all species	all species	all species
reduced number				
mandibular formula				some species
frontal sutures				most species
anelli:				many species
reduced number				
mesoscutum:				some species
median groove				
scutellum:				some species
median groove				
hairs on propodeal callus:			many species	many species
reduced number				
hairs on submarginal vein:			some species	all species
reduced number				
fore tibial spur bifid (LaSalle <i>et al.</i> 1997)		some species (at least)	some species (at least)	some species (at least)
short stigmal vein		most species		all species
short postmarginal vein		most species	most species	most species
lines of hairs figuring Rs1, & r-m		most species		some species
hosts: Agromyzidae	several species	a few species	a few species	several species

restricted to the ventral edge; propodeum with a subspiracular tubercle; marginal vein relatively long; stigmal vein relatively short (Boucek 1988; Schauff 1991). Unfortunately, many of these characters are absent in *Trisecodes*. There are 3 pairs of very small setae on the scutellum, only a single seta on the dorsal surface of the submarginal vein, and no subspiracular spiracle. Also the notauli are complete, an-

other character which is unusual but not unknown in the Entedoninae. However, exceptions are known to all of the characters listed above (see Ubaidillah *et al.* 2000 for some examples), and *Trisecodes* does possess one very strong character to support it as an entedonine, the shape and placement of the frontal sutures. Additionally, one genus of Entedoninae, *Asecodes*, which includes species previously

placed in *Teleopteris* (Hansson 1996), may have the forewing with almost identical lines of setae radiating from the stigmal vein. However, it is doubtful that there is a close relationship between *Trisecodes* and *Asecodes* based on other characters, such as the strength of the sculpturing in *Trisecodes*.

ACKNOWLEDGMENTS

We are grateful to Dr. O. T. Lewis who provided most of the material used for the description of the *Trisecodes* and for the information on its biology. We also thank Dr. C. Hansson and Dr. J. Pinto for discussion about the placement of *Trisecodes agronyzae* and useful comments on the manuscript.

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Description of a New Genus of Entedoninae (Hymenoptera: Eulophidae) from the Neotropical Region, Including Three New Species

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Abstract.—*Acanthala* gen.n. including three new species, *albiclava*, *plaumanni*, *pubipennis*, of the subfamily Entedoninae (Hymenoptera: Eulophidae) is described from the Neotropical Region (Belize, Brazil and Costa Rica). *Acanthala* is unique among Eulophidae by having the forewing with a row of strong setae on the dorsal surface of the marginal vein. The three species are known only from the female sex and nothing is known about their biology.

The Eulophidae has a worldwide distribution and is one of the largest families of Chalcidoidea. The knowledge of the group is unevenly distributed, with a strong displacement towards the northern hemisphere, although the group is expected to be more species rich in tropical areas. Estimates of the eulophid fauna in the New World tropics corroborates this (e.g. Gaston *et al.* 1996, LaSalle and Schauff 1995), but very little is known about the eulophid fauna of this region.

To increase our knowledge of eulophids in general, and of the eulophid fauna in the Neotropical region in particular, a new genus with unique morphological features is described below. The descriptions of three new species belonging to the new genus are also included. Unfortunately information regarding the biology is not yet known.

Acronyms of museums used in the text are as follows: BMNH: The Natural History Museum, London; CNC: Canadian National Collections of Insects and Arachnids, Ottawa; INBio: Instituto Nacional de Biodiversidad, Santo Domingo, Costa Rica; LUZM: Lund University Zoology Museum, Sweden; MIUCR: Museo de Insectos, Universidad de Costa Rica; USNM: United States Museum of Natural History, Washington, D.C.

Acanthala Hansson, new genus

Type species.—*Acanthala pubipennis* Hansson, new species.

Diagnosis.—Dorsal surface of marginal vein with a row of strong setae (Figs. 1, 8); eyes hairy (Figs. 1, 6, 7); mandibles with a single tooth at apex (Fig. 7); frontal cross-groove incomplete, not reaching eyes (Fig. 6), or missing (Fig. 7); pedicel conspicuously hairy on dorsal surface (Figs. 2–4); mesoscutum and scutellum with small-meshed and strong reticulation (Fig. 1), hence dull.

Description.—Flagellum with sensilla ampullacea short and symmetric, present on all segments. Antenna with 2–3 anelli. Mandibles with a single tooth at apex. Clypeus weakly delimited laterally, but not delimited dorsally. Antennal scrobes join on frontal cross-groove (or cross-groove missing). Frontal cross-groove V-shaped, not reaching eyes, or missing. Eyes hairy. Occiput with a weak median groove in upper part, close to occipital margin (*plaumanni*, *pubipennis*), or median groove missing (*albiclava*). Pronotum well developed and clearly visible in dorsal view, without transverse carina. Midlobe of mesoscutum with two pair of strong setae; notauli not visible (*plaumanni*, *pubipen-*



Fig. 1. *Acanthala pubipennis* habitus.

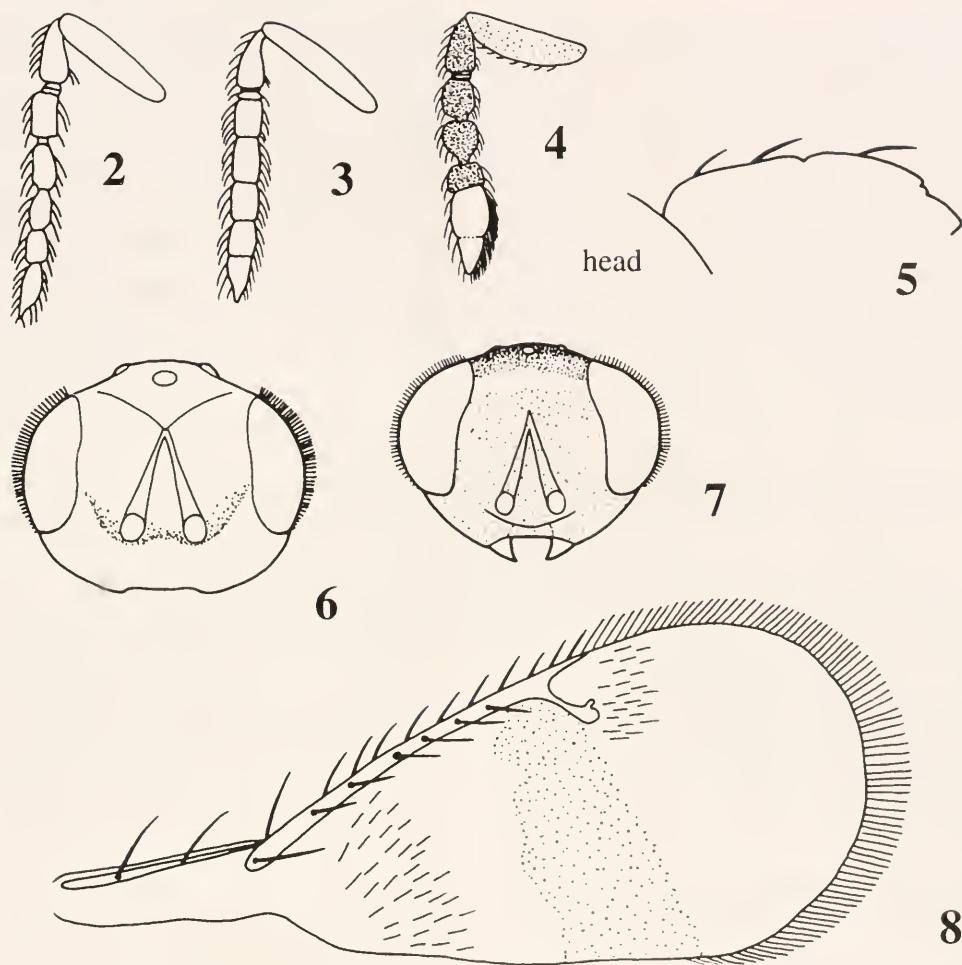
nis), or indicated in anterior 1/2 (*albiclava*). Scutellum with one pair of strong setae, situated at equal distance from anterior and posterior margins of scutellum (*pubipennis*) or closer to anterior margin (*albiclava*, *plaumanni*). Transepimeral sulcus (i.e. the sulcus separating upper and lower mesepimeron) almost straight (*pubipennis*, *albiclava*) or curved (*plaumanni*). Dorsellum visible in dorsal view. Propodeal callus with two setae. Forewing rounded; costal cell narrow; postmarginal vein $0.8-1.6\times$ as

long as stigmal vein; speculum open (*albiclava*, *plaumanni*) or closed (*pubipennis*) below; radial cell bare, without stigmal hairlines. Petiole short, hardly visible in dorsal view, and transverse.

Biology.—Not known.

Distribution.—Neotropical region (Belize, Brazil, Costa Rica).

Etymology.—Named after the row of strong spinelike setae on dorsal surface of marginal vein: *acanth-ala* = spiny wing. The gender is regarded as feminine.



Figs. 2–8. *Acanthala* spp. females. 2–4, antenna in lateral view: 2, *A. pubipennis*; 3, *A. plaumanni*; 4, *A. albiclava*. 5, thoracic dorsum in lateral view of *A. pubipennis*. 6–7, head in frontal view: 6, *A. pubipennis*; 7, *A. albiclava*. 8, forewing of *A. albiclava*.

Discussion.—The dorsal row of setae on the marginal vein is a unique character state for *Acanthala* within the Eulophidae, and hence a strong apomorphy. The mandibles with a single apical tooth is also unique to *Acanthala*. A similar character state is present in some species of *Paracrias* Ashmead, but different from *Acanthala* since in *Paracrias* there is a single large tooth and a small second tooth dorsally (Fig. 14 in Schauff 1985). Another apomorphy present in *Acanthala* is the incomplete or missing frontal cross-groove. However, this apomorphy is present in

several entedonine genera, e.g. in some species of *Chrysocharis* Förster, in most species of *Entedon* Dalman, in *Entedononecremnus* Girault and *Eprhopalotus* Girault. The occurrence among genera not otherwise shown to be closely related (e.g. Schauff 1991, LaSalle & Schauff 1994) does not indicate a high information value with regard to relationship.

The dorsal row of strong setae on marginal vein and the dense and strong but still fine reticulation on vertex and thoracic dorsum makes *Acanthala* easily recognizable, habitually not resembling any

other entedonine genus from the Neotropical region.

In Boucek (1988) *Acanthala* runs either to *Chrysocharis* (couplet 149), or to *Chrysotomyia* (couplet 153). In Schauff et al. (1997) *Acanthala* runs either to couplet 126 (*Chrysocharis* or *Grahamia*) or (with some difficulties, due to the fact that *Acanthala* does not possess the complete combination of characters presented in the couplets) to either *Asecodes* (couplet 132) or to

Neochrysocharis (couplet 134). However, the row of strong setae on dorsal surface of marginal vein makes *Acanthala* easy to separate from above mentioned genera, and from any other entedonine genera. Note: the first character used under couplet 134 in Schauff et al. (1997), the shape of the transepimeral sulcus has been confused: *Closterocerus* has a strongly arched sulcus while *Neochrysocharis* has a weakly curved or straight sulcus! (Hansson 1995).

KEY TO FEMALES OF ACANTHALA

1. Predominantly yellowish-brown nonmetallic species; antenna with a distinct antennal clava (Fig. 4), clava white and remaining flagellum brown; frontal cross-groove missing (Fig. 7) *albiclava* new species
- Predominantly dark and \pm metallic species; antenna without distinct clava (Figs. 2, 3), flagellum completely pale brown; frontal cross-groove present medially (Fig. 6) 2
2. Forewing (Fig. 1) with comparatively dense setation, speculum closed below; flagellum narrower, e.g. flagellomeres II and III $2\times$ as long as wide, and with more distinct constrictions between flagellomeres (Fig. 2) *pubipennis* new species
- Forewing with comparatively sparse setation (as in *albiclava* (Fig. 8)), speculum open below; flagellum stouter, e.g. flagellomeres II $1.7\times$ and III $1.4\times$ as long as wide, and with less distinct constrictions between flagellomeres (Fig. 3) *plumanni* new species

Acanthala albiclava Hansson, new species

(Figs. 4, 7, 8)

Diagnosis.—Predominantly yellowish-brown nonmetallic, with only major part of vertex and upper 1/2 of occiput metallic (bluish-purple); antenna (Fig. 4): scape comparatively wide, $3.8\times$ as long as median width, yellowish-brown; pedicel and flagellomeres 1–3 brown, flagellomeres 4–5 white with ventral surface densely setose, flagellum with a distinct clava; without frontal cross-groove (Fig. 7); setae on vertex and thoracic dorsum comparatively thin, as thick as setae on marginal vein; compared to *pubipennis* (Fig. 1), forewing in *albiclava* (Fig. 8) with sparse setation (wing surface distad of speculum with same setation, Fig. 8 only shows setation below base of marginal vein and on surface just distad of postmarginal and stig-

mal veins), speculum open below (i.e. cubital hairline missing below speculum), hind margin of forewing strongly curved upwards just below base of marginal vein; anteromedian part of propodeum strongly raised into a peak; propodeum with a complete median carina that splits in two carinae in posterior part; propodeal surface reticulate.

Female.—Length of body = 0.9–1.0 mm. **Colour.** Scape yellowish-brown; pedicel and flagellomeres 1–3 brown, flagellomeres 4–5 white. Frons yellowish-brown, with a white stripe from eye to eye along upper border (Fig. 7). Vertex yellowish-brown in front of anterior ocellus, remaining vertex metallic bluish-purple. Upper 1/2 of occiput metallic bluish-purple, lower 1/2 yellowish-brown. Mesosoma, including legs, yellowish-brown. Forewing with a weak infusate stripe below stigmal vein, stripe reaches hind margin of wing.

Gaster yellowish-brown. **Head:** Antenna as in Fig. 4; with three discoid anelli. Ratios height of eye/malar space/width of mouth: 2.1/1.0/1.4. Frons with rather strong small-meshed reticulation, meshes isodiametric. Vertex dull, with strong small-meshed reticulation. Ratios distances between posterior ocelli/one posterior ocellus and eye/posterior ocelli and occipital margin: 2.0/1.0/1.0. Occiput without a weak median groove in upper part; occipital margin rounded. Ratio width of head/width of thorax (measured across mesoscutum, just in front of base of forewing) = 1.2. **Mesosoma:** Mesoscutum and scutellum dull, with rather strong small-meshed reticulation, meshes on mesoscutum isodiametric, on scutellum slightly elongate. Dorsellum concave and strongly reticulate with small meshes. Forewing speculum open below; ratio length of postmarginal vein/length of stigmal vein = 0.8; ratios length of wing (measured from base of marginal vein to the point along outer margin of forewing farthest away from base of marginal vein)/length of marginal vein/height of wing: 1.9/1.0/1.0. Anteromedian part of propodeum strongly raised into a peak, with a complete median carina that splits in two carinae in posterior part; propodeal surface reticulate with small meshes. **Metasoma:** Gaster ovate; ratio length of mesosoma/length of gaster = 0.7–0.8.

Type material.—Holotype female: BRAZIL: Bahia Itabuna, 11–14.ii.1984, F. Benton (deposited in BMNH). Paratypes: Two females with same label data as holotype (1 female in BMNH, 1 female in LUZM); from same locality as holotype but collected iv.1983 (1 female, in BMNH), 2–6.v.1983 (1 female, in USNM), viii.1983 (1 female in BMNH, 1 female in LUZM).

Etymology.—Named after white antennal clava: albi-clava = white club.

***Acanthala plaumanni* Hansson, new species**
(Fig. 3)

Diagnosis.—Predominantly dark and metallic species; entire antenna brown,

scape comparatively narrow, $5.7\times$ as long as median width (Fig. 3), flagellum without distinct clava, flagellomeres stout and with less distinct constrictions between them; head shrivelled in type series, but frontal cross-groove visible at least medially; setae on vertex and thoracic dorsum comparatively strong, about twice as thick as setae on marginal vein (as in *pubipennis* (Fig. 5)); hind margin of forewing not strongly curved upwards below base of marginal vein (as in *pubipennis* (Fig. 1)); forewing with comparatively (compared to *pubipennis* (Fig. 1)) sparse setation (as in *albiclava* (Fig. 8)), speculum open below (as in *albiclava* (Fig. 8)); propodeum with weak reticulation, smooth and shiny in some places.

Female.—Length of body = 0.8 mm (in both type-specimens). **Colour:** Antenna pale brown. Frons golden-green. Vertex metallic bluish-purple. Occiput golden. Mesoscutum golden-green. Scutellum metallic purple in median 1/2, golden-green in lateral 1/4 in holotype; paratype with entire scutellum golden-green. Propodeum golden-green. Fore and hind coxae dark and metallic, mid coxa infusate; femora infusate; tibiae and tarsi pale. Forewing weakly infusate below marginal vein, infuscation reaching to hind margin of wing. Gaster golden-purple. **Head:** Antenna as in Fig. 3; with one discoid and one slightly larger anellus. Ratios height of eye/malar space/width of mouth: 1.9/1.1/1.0. Frons with rather weak small-meshed reticulation, meshes \pm isodiametric. Vertex with weak reticulation, shiny. Ratios distances between posterior ocelli/one posterior ocellus and eye/posterior ocelli and occipital margin: 1.7/1.0/1.0. Occiput with a weak median groove in upper part, close to occipital margin; occipital margin rounded. Ratio width of head/width of thorax (measured across mesoscutum, just in front of base of forewing) = 1.0. **Mesosoma:** Mesoscutum and scutellum dull, with rather strong small-meshed reticulation, meshes isodiametric.

Dorsellum concave and reticulate. Forewing speculum open below; ratio length of postmarginal vein/length of stigmal vein = 1.4; ratios length of wing (measured from base of marginal vein to the point along outer margin of forewing farthest away from base of marginal vein)/length of marginal vein/height of wing: 2.0/1.2/1.0. Propodeum with weak reticulation, smooth and shiny in some places. **Metasoma:** Gaster ovate; ratio length of mesosoma/length of gaster = 0.9–1.0.

Type material.—Holotype female: BRAZIL: Santa Catarina, Nova Teutonia, xi.1949, F. Plaumann (deposited in BMNH). Paratype: One female from same locality as holotype but collected ix.1943 (in BMNH).

Etymology.—Named after F. Plaumann, collector of type series.

***Acanthala pubipennis* Hansson, new species**

(Figs. 1, 2, 5, 6)

Diagnosis.—Predominantly dark and metallic species; entire antenna brown, scape comparatively narrow (Fig. 2), $4.7\times$ as long as median width, flagellum without distinct clava, flagellomeres slender and with distinct constrictions between them; setae on vertex and thoracic dorsum comparatively strong, about twice as thick as setae on marginal vein (Fig. 5); frontal cross-groove present, missing only close to eyes (Fig. 6); forewing (Fig. 1) with comparatively dense setation, speculum small and closed below, cubital hairline curved upwards towards base of marginal vein; hind margin of forewing not strongly curved upwards below base of marginal vein; propodeum smooth and shiny (Fig. 1).

Female.—Length of body = 0.7–1.0 mm. **Colour:** Antenna pale brown. Frons dark with weak golden tinges. Vertex dark with weak metallic tinges. Occiput dark with metallic tinges. Mesoscutum, scutellum and propodeum dark with golden-purple tinges. Fore and hind coxae dark, mid

coxa pale; femora dark; tibiae and tarsi infusate. Forewing weakly infusate below marginal vein, infuscation reaching to hind margin of wing. Gaster golden-purplish. **Head:** Antenna as in Fig. 2; with two discoid anelli. Ratios height of eye/malar space/width of mouth: 1.6/1.0/1.0. Frons with rather weak small-meshed reticulation, meshes transverse. Vertex dull, with strong small-meshed reticulation. Ratios distances between posterior ocelli/one posterior ocellus and eye/posterior ocelli and occipital margin: 2.0/1.7/1.0. Occiput with a weak median groove in upper part, close to occipital margin; occipital margin rounded. Ratio width of head/width of thorax (measured across mesoscutum, just in front of base of forewing) = 0.9. **Mesosoma:** Mesoscutum and scutellum dull, with rather strong small-meshed reticulation, meshes isodiametric. Dorsellum convex and reticulate with small meshes. Forewing speculum small and closed below, cubital hairline curved upwards towards base of marginal vein; ratio length of postmarginal vein/length of stigmal vein = 1.6; ratios length of wing (measured from base of marginal vein to the point along outer margin of forewing farthest away from base of marginal vein)/length of marginal vein/height of wing: 1.8/1.1/1.0. Propodeum smooth and shiny; propodeal callus with small-meshed reticulation. **Metasoma:** Gaster ovate; ratio length of mesosoma/length of gaster = 0.8–1.0.

Type material.—Holotype female: BELIZE: Las Cuevas, ix.1995, T. King & A. Howe (deposited in BMNH). Paratypes: Following from same locality as holotype but collected iv.1995 (1 female, in LUZM), vi.1995 (1 female, in BMNH); 1 female COSTA RICA: Alajuela, Peñas Blancas, 700m, ii.1987, E. Cruz (in CNC); 1 female COSTA RICA: Guanacaste, P.N. Santa Rosa, 300m, 20.xii.1986–10.i.1987, D.H. Janzen & I.D. Gauld (in BMNH); following from same locality as previous but collected 31.i–21.ii.1987 (1 female, in USNM),

16.v-6.vi.1987 (1 female, in INBio); 1 female COSTA RICA: Puntarenas, Golfo Dulce, 3km SW Rincón, 10m, vii.1991, P. Hanson (in MIUCR).

Etymology.—Named after densely setose forewing; pubi-pennis = hairy wing.

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The Identity of *Pteroptrix imitatrix* (Fullaway) (Hymenoptera: Aphelinidae)

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Abstract.—Taxonomic notes are provided on two aphelinid wasps, *Pteroptrix imitatrix* (Fullaway), described from Hawaii, and *Pteroptrix albifemur* (Girault), described from Australia. The former is shown to be a synonym of the latter. New taxonomic, distributional and biological data are provided.

Among several Aphelinidae collected in the Galapagos Islands by Dr John Heraty (UCR) were three specimens of a *Pteroptrix* species belonging to the *maritima*-group *sensu* Viggiani and Garonna (1993). This species-group formerly comprised part of the genus *Archenomus*, and using the key to world species of *Archenomus* by Prinsloo and Naser (1990) the specimens were identified by the first author as *Pteroptrix* (= *Archenomus*) *albifemur* (Girault). Consulting the description of *P. imitatrix* (Fullaway) and non-type material of that species at the United States National Museum, it became apparent that the specimens from the Galapagos were also very close, if not identical, to that species. Prinsloo and Naser did not treat *P. imitatrix* as the type was not located by them. *P. imitatrix* was described from Hawaii, and after consultation with Mr G. Nishida of the Bishop Museum the type material was finally located by Mr B. Kumashiro at the Department of Agriculture. We have compared the types of *P. albifemur* (Girault), *P. imitatrix* (Fullaway) and the Galapagos (Ecuador) material, and find them to be conspecific. Subsequently, material from Florida, Puerto Rico and India was also found to belong to *P. albifemur*. The following synonymy, redescription, lecto-

type designation and distributional information are published to clear up some of the many taxonomic problems that still exist in this genus.

Terminology follows Hayat (1983) except that the terms mesosoma and metasoma replace thorax plus propodeum, and gaster, respectively. Abbreviations of depositories can be found under "Acknowledgments".

Pteroptrix albifemur (Girault 1915) (Figs. 1–3)

Apteroptrix albifemur Girault 1915: 65.

Archenomus albifemur (Girault): Prinsloo and Naser 1990: 23.

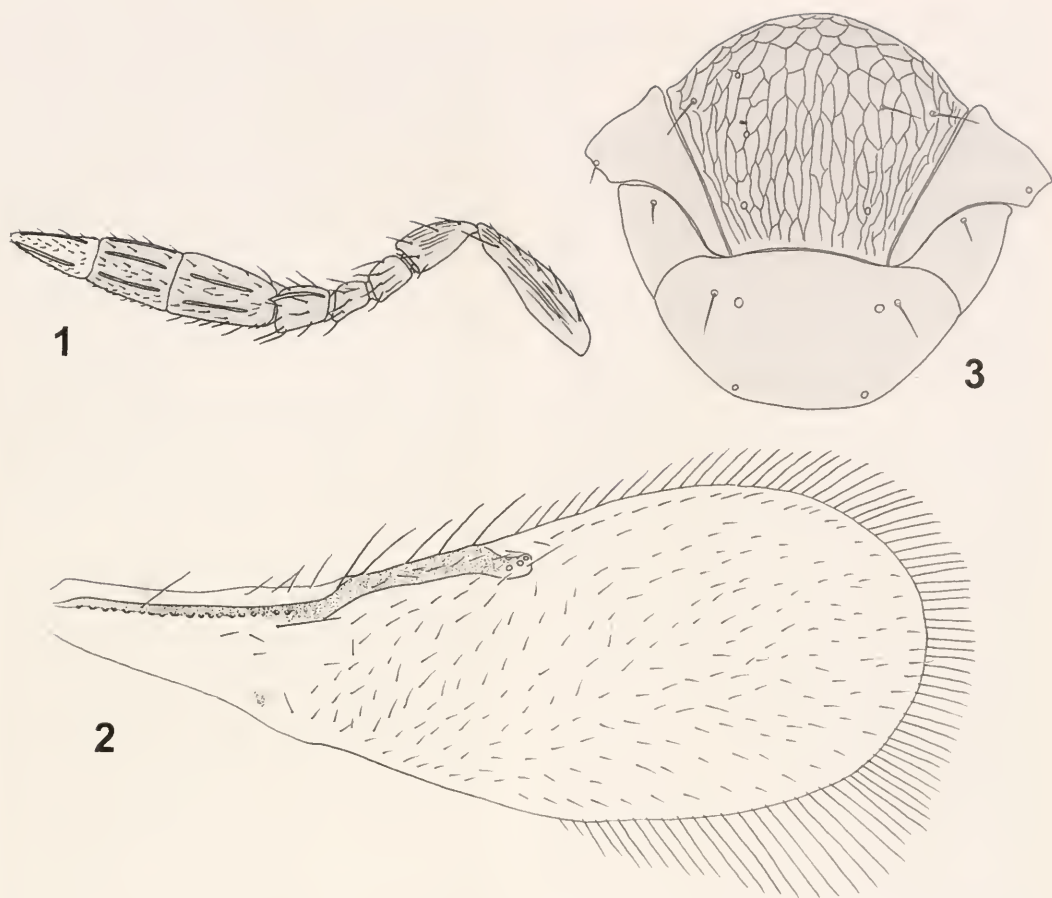
Pteroptrix albifemur (Girault): Viggiani and Garonna 1993: 61; Hayat 1998:245.

Pseudopteroptrix imitatrix Fullaway 1918: 464.
Syn. nov.

Archenomus imitatrix (Fullaway): Prinsloo and Naser 1990: 23.

Pteroptrix imitatrix (Fullaway): Viggiani and Garonna 1993: 60.

Female.—**Colour:** Antenna with flagellum pale brown, the scape with its outer edge darker brown, radicle dark brown. Head with the lower occiput, genae and stemmaticum dark brown, the eye margins darkest, frons and upper occiput paler brown. Mesosoma brown, the scutel-



Figs. 1–3. *Pteroptrix albifemur*, female. 1, Antenna. 2, Fore wing. 3, Mesonotum, showing sculpture of mesoscutal mid lobe (specimen from Santa Cruz, Galapagos).

lum strikingly white, side lobes and border of mesoscutum paler brown. Legs white, the hind coxa and leading edge of the hind femur slightly darkened. Wings hyaline, slightly darkened below the marginal vein. Metasoma brown. **Morphology:** Mandibles with two teeth and a truncation. Antennal formula 1,1,3,3 (fig. 1); scape slightly more than $2 \times$ pedicel length. Funicle segments all longer than wide, subequal in length. F2 slightly the shortest; funicle about $0.5 \times$ length of club. Flagellum with the following numbers of longitudinal sensilla: F1: 0; F2: 0; F3: 0–1; F4: 3–4; F5: 3–4; F6: 3. Mid lobe of mesoscutum (fig. 3) with 6–7 setae, each lateral lobe with 1, each axilla with 1, and

scutellum with 4. Fore wing (fig. 2) with 1 seta on submarginal vein, 2–4 setae in basal cell. Anterior margin of marginal vein with 5–6 setae, and one large seta at the junction of the submarginal vein and parastigma. Maximum width of wing $2.6\text{--}2.9 \times$ longest seta on marginal fringe. Length of second valvifers $3.3\text{--}3.6 \times$ third valvulae. Second valvifer and third valvula combined $1.1 \times$ length mid tibia. Metasoma oval, longer than wide and about $1.5 \times$ length mesosoma. Terga II–VII with 0, 1+1, 1+1, 1+1, 1+2+1 and 1+2+1 setae respectively.

Male.—Unknown

Variation.—Insignificant in the material examined.

Material examined.—Type material: Holotype female *Apteroptrix albifemur* Girault [AUSTRALIA: Cairns, Gordonvale] Type HY/2962 (3894) (QM). Lectotype female (here designated) *Pseudopteroptrix imitatrix* Fullaway [HAWAII:] Honolulu. 17.i.[19]18 ex *Howardia biclavis* (HDA, slide-mounted); paralectotypes, 5 females: 1 female [HAWAII:] Honolulu, Oahu, 12.i.18 (D.T. Fullaway) *Howardia biclavis* (BMNH, slide-mounted). [HAWAII:] Honolulu, Oahu, 4.ii.18 (D.T. Fullaway) *Howardia biclavis* (1 female HDA, card-point; 1 female USNM slide-mounted). [HAWAII:] Tantalus, el. 1300 ft (J. Kotinsky) *H. biclavis* (2female, HDA). Additional material: ECUADOR: Galapagos, Santa Cruz, Darwin Sta. 20m PAN 14–18.v.91 (J. Heraty) arid zone (1female, BMNH). ECUADOR: Galapagos, Isabela, C. Azul, 3 Km W Cal. Iguana 200 m 25.v.91 (J. Heraty) deciduous forest H91/061 (1 female, BMNH). ECUADOR: Galapagos, Isabela, Alcedo 7 Km SW NE Playa 600 m 25.vi.91 (J. Heraty) arid forest H91/118 (1 K, BMNH). ECUADOR: Fernandina, 5 Km NE Cabo Hammon 110 m 4–10.v.91 (J. Heraty) pan. Palo Santo forest H91/031 (1 female, USNM). INDIA: Karnataka, 25 Km W. of Mudigere 28.x. – 3.xi.1979 J.S. Noyes (1 female, BMNH; Hayat det.). PUERTO RICO: Indiera 9–10.iii.1936 H.L. Dozier “ex *Howardia biclavis* on sapotaceous tree, *Lucuma* sp.” (7 female, USNM). PUERTO RICO: Mayaguez 18.x.1935 H.L. Dozier “sweeping Roble and roadside vegetation at 1000 ft” (1 female, USNM). PUERTO RICO: Rio Piedras 3.ix.1912 T.H. Jones “from twig of achiote, *Bixa orellana*, on which *Howardia biclavis* was present” (1 female, USNM). USA: Florida, Oneco J.W. Collins 2.ix.1922 (1female, USNM).

Host.—Diaspididae: *Howardia biclavis* (Comstock). A pantropical, polyphagous species (Williams and Watson, 1988) occasionally recorded as a pest, for example of citrus (Grillo *et al.*, 1983). The “eulophid” parasite of *H. biclavis* recorded by the latter authors could well be *P. albifemur*.

Fullaway (1918) mentioned a slide-mounted specimen reared from *Hemiberlesia* (as *Aspidiotus*) *rapax* (Comstock). This specimen has not been seen by us.

Distribution.—Australia, Ecuador, Hawaii (and presumably widespread in the Pacific), India, Puerto Rico, USA (Florida).

Discussion.—*Pteroptrix albifemur* belongs to the *maritima*-group of *Pteroptrix*, where it was correctly placed by Viggiani and Garonna (1993). This group is characterized by lacking the complete sulcus above the occipital foramen and antennal formula of female 1.1.3.3. Viggiani and Garonna (1993) were mistaken in suggesting that *P. imitatrix* belongs to the *bicolor*-group. Prinsloo and Naser (1990) placed *albifemur* in their *peratus*-group, and suggested *imitatrix* could belong to their *incolus*-group. These last-mentioned species groups were combined into the *maritima*-group, following the redefinition of species groups by Viggiani and Garonna (1993), a step that was necessitated by the incorporation of *Archenomus* into *Pteroptrix*. *Pteroptrix albifemur* is morphologically close to the following species in the *maritima*-group: *P. opaca* Erdős, *P. patriciae* (Prinsloo and Naser) and *P. abnormis* (Prinsloo and Naser). We have not examined type material of *P. opaca* (described from Hungary), which appears to be lost (J. Papp, personal communication). We have, however, examined specimens from Hungary (though not from the type locality) and from Italy, which agree in all respects with the original description. *Pteroptrix opaca* differs from *P. albifemur* most strikingly in the colour of the legs (tibiae and femora dark in *P. opaca*, very largely pale in *P. albifemur*). The wing of *P. opaca* is much more deeply infuscated below the marginal vein than in *P. albifemur*, as well as being noticeably more densely setose. *Pteroptrix abnormis* also differs from *P. albifemur* in the colour and setation of the fore wings, although the legs and antennae are very similar in colour and proportions to those of *P. albifemur*. The sculpture

of the face and mesoscutum of *P. abnormis* is, however, much less pronounced than in *P. albifemur*. Differences between *P. patriciae* and *P. opaca* are slight, being restricted largely to the colour of the legs (although the F1 and F3 of the female antenna in *P. patriciae* are slightly longer than those of *P. opaca*). In this respect, *P. patriciae* is somewhat intermediate between *P. opaca* and *P. albifemur*. We suggest that a thorough review of the species comprising the *maritima*-group of *Pteroptrix* be carried out before synonymising any of these species based on the limited material available during this study.

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A Review of the *Sphex flavipennis* Species Group (Hymenoptera: Apoidea: Sphecidae: Sphecini)

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Abstract.—The *Sphex flavipennis* species group, a Palearctic assemblage formerly called the *maxillosus* species group, is characterized, its species are diagnosed, keyed, their distributions summarized, and male antennae illustrated. The large Eurasian wasp formerly known as *maxillosus* Fabricius or *rufocinctus* Brullé must now be called *funerarius* Gussakovskij. Similarly, the species formerly known as *afer* Lepeletier must now be called *leuconotus* Brullé. The following species are included (**new synonyms** are listed in parentheses): *atropilosus* Kohl, 1885; *flavipennis* Fabricius 1793 (*rufocinctus* Brullé 1833); *funerarius* Gussakovskij 1934 (*maxillosus* Fabricius 1793, a junior homonym of *Sphex maxillosus* Poiret 1787; *obscurus* Fischer de Waldheim 1843; and *mavromoustakisi* de Beaumont 1947); *leuconotus* Brullé 1833 (*triangulum* Brullé 1833, a junior homonym of *Sphex triangulum* Villers 1789; *afer* Lepeletier 1845; *sordidus* Dahlbom 1845; *tristis* Kohl 1885; *plumipes* Radoszkowski 1886, a junior homonym of *Sphex plumipes* Drury 1773; and *pachysoma* Kohl 1890); *libycus* de Beaumont 1956; *melas* Gussakovskij 1930; and *oxianus* Gussakovskij 1928 (*nubilis* de Beaumont 1968). A lectotype is designated for *Sphex funerarius* Gussakovskij 1930, and a neotype is designated for *Sphex leuconotus* Brullé 1833. Descriptive notes are provided for the type material of *Sphex atropilosus* Kohl, *funerarius* Gussakovskij, *leuconotus* Brullé, *rufocinctus* Brullé, and *triangulum* Brullé.

It is rather ironic, after all these years, that the proper scientific names have not been established for *Sphex maxillosus* Fabricius 1793 and *afer* Lepeletier 1845, since these represent two of the largest Palearctic sphecids wasps. This problem is corrected here. Initially our study was prompted by Menke's examination in 1964 of Brullé's type specimens at the Muséum National d'Histoire Naturelle, Paris, which suggested that two taxa recognized by Kohl (1890) as synonyms of *maxillosus* (*rufocinctus* Brullé and *triangulum* Brullé) were not conspecific with that species. This was corroborated by Pulawski in 1975, who re-examined the same material.

In 1994 both of us restudied the types and confirmed our prior assessments of them. These were important findings because van der Vecht (1959) noted that *maxillosus* Fabricius was a junior homonym and the species needed a replacement name. Van der Vecht believed that *leuconotus* Brullé was the oldest available replacement for *maxillosus*. However, we are certain that *leuconotus* is a senior synonym of *afer* Lepeletier. In this paper we establish that *funerarius* Gussakovskij is the proper name for *maxillosus* Fabricius and *leuconotus* Brullé the proper name for *afer* Lepeletier.

Our study has enabled us to construct an identification key to the Palearctic species of the *flavipennis* group. This key should be regarded as provisional because these wasps are taxonomically difficult, and we have not made an exhaustive

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study of the species. Too little is known about geographic variation in the *flavipennis* group, particularly the color of the wings, setation, legs, and gaster. These may prove to be variable within some species, but a very large specimen database would be required to resolve species limits and the significance of geographic variation. The apparent variation in male placoid distribution on the antenna also needs to be carefully analyzed, as well as possible variation in the male genitalia. Currently the male genitalia seem identical or nearly so in the taxa we discuss here.

The family group names used in the title are based on Melo (1999).

SOURCES OF MATERIAL

Abbreviations used to indicate location of specimens are listed below with corresponding institutions.

CAS: California Academy of Sciences, San Francisco, California, U.S.A.

Copenhagen: Zoologisk Museum, Copenhagen, Denmark

Dresden: Staatliches Museum für Tierkunde, Dresden, Germany

Genova: Museo Civico di Storia Naturale "Giacomo Doria", Genova, Italy

Kraków: Instytut Systematyki i Ewolucji Zwierząt, Polska Akademia Nauk, Kraków, Poland

Lausanne: Musée Cantonal de Zoologie, Lausanne, Switzerland

Lund: University of Lund, Lund, Sweden

Menke: A. S. Menke Collection, Amphipha Research Institute, Bisbee, Arizona, U.S.A.

Moscow: Zoological Museum, Moscow State University, Moscow, Russia

Palermo: Istituto di Zoologia, Università di Palermo, Palermo, Italy

Paris: Muséum National d'Histoire Naturelle, Paris, France

Stockholm: Naturhistoriska Riksmuseet, Stockholm, Sweden

St. Petersburg: Zoological Institute, Rus-

sian Academy of Sciences, St. Petersburg, Russia

USNM: United States National Museum of Natural History, Washington D.C., U.S.A.

Wien: Naturhistorisches Museum, Wien, Austria

Zürich: Entomologisches Institut, Eidgenössische Technische Hochschule, Zürich, Switzerland

METHODS

Morphological terms used here follow Bohart and Menke (1976) except that we follow Salmon (1929) for the name of the curved, cord-like "tendon" at the base of the petiole. Salmon called this the funicle, and we adopt his term because it is not a tendon in the true sense of the word.

Measurements of the abdominal petiole are made as follows: the width is measured at the base of tergum I, the length is measured from the base of the funicle (on the petiole) to the base of tergum I.

When describing color we use the term "red" to indicate non-black areas of the legs. In reality, the true color more closely approximates amber, or reddish brown in many instances. Setal color is described as pale or white vs. dark brown or black. In some cases, pale or white setae are really silver.

For the uncommonly collected species we have listed locality records known to us.

The fourth edition of the International Code of Zoological Nomenclature (ICZN 1999) stipulates in Article 74.7.3 that "to be valid, a lectotype designation made after 1999 must contain an express statement of the taxonomic purpose of the designation". These statements must accompany each designation (Article 74.3). Traditionally lectotype designations have been indicated by the words "present designation" and the purpose is clear to all, namely to fix the identity of the name involved. To add a statement after each designation seems redundant and repetitive

to us, but to satisfy the Code, we have followed "present designation" with the following statement "in order to ensure the name's proper and consistent use".

The *flavipennis* Species Group

The species discussed here belong to a lineage that de Beaumont (1960) called the *maxillosus* group. Because *maxillosus* is a junior homonym, we have renamed it the *flavipennis* group, using the oldest valid species name.

Females of the *flavipennis* group share the following defining characters: clypeal disk conspicuously convex, but abruptly depressed near free margin, delimiting a narrow, flat rim; labral apex with inverted Y- or V-shaped carina whose arms project as small lobes; base of Y or V often extending as a median carina toward labral base. In addition to these apparently derived characters, the species lack certain specializations of other *Sphex*: the metanotum is simple (not bituberculate); the propodeal dorsum lacks coarse, widely spaced, transverse carinae or wrinkles; and the propodeal side lacks a vertical swelling anterior to the spiracular groove. Males apparently lack features of species group significance.

The group contains the following Palearctic species: *atropilosus* Kohl 1885, *flavipennis* Fabricius 1793, *funerarius* Gussakovskij 1934 (= *maxillosus* Fabricius 1793, nec Poiret 1787; *rufocinctus* of authors after 1975), *leuconotus* Brullé 1833 (= *afer* Lepeletier 1845), *libycus* de Beaumont 1956, *melas* Gussakovskij 1930, and *oxianus* Gussakovskij 1928.

In addition to the seven species listed above we have studied three males and one female from Morocco collected at Aït-Saouin (between Ouarzazate and Agdz) southwest of the Jbel Sarhro Mts. (CAS) that may be a new species or an extreme form of one of the currently known species. They resemble *flavipennis* and *funerarius*, but the male antenna has broad placoids on flagellomeres IV-VI, and the fla-

gellomeres are more elongate than in those two species. The female mid and hindlegs are black, but the foretibia and tarsus are reddish.

Species discrimination in the *flavipennis* group is difficult, especially in females. Previous authors have used wing color, setal color, presence or absence of long setae on the femora, and proportions of the petiole and/or comparisons of its length with the length of one of the hindtarsomeres to separate females of some species. However, the separation of females of *flavipennis*, *funerarius*, and *oxianus* is particularly vexing, and association with males may often be the only reliable way to identify these species. The most useful male character is the number and width of placoids on the flagellum (although they are variable in *funerarius* especially; see that species below for details). Other male features that have been used by previous workers are the length of the lateral setal brushes of sternum VII, the form of the clypeal free margin, and color pattern. Generally, however, these characters are not wholly reliable. Male genitalia lack the unusual elaborations found in some sections of the genus and appear identical in species of the *flavipennis* group. The penis valve head is arcuate in lateral profile and is armed ventrally with a row of teeth.

The following authors provide keys, records, and other valuable information on species in the *flavipennis* group: Kohl (1890), worldwide revision of genus; Dusmet and Mercet (1906), Spanish species; Roth (1925), North African species; Berland and Bernard (1949), French species; de Beaumont (1951), Moroccan species, and (1960), placoids of male antenna; Scobiola (1960), Romanian species; Kazenas (1978), Kazakh species; Pulawski (1978), species of the European part of former USSR; Mingo and Gayubo (1984), Spanish species; Hamon, Fonfria, and Tussac (1991), French species; and Bitsch et al. (1997), western European species.

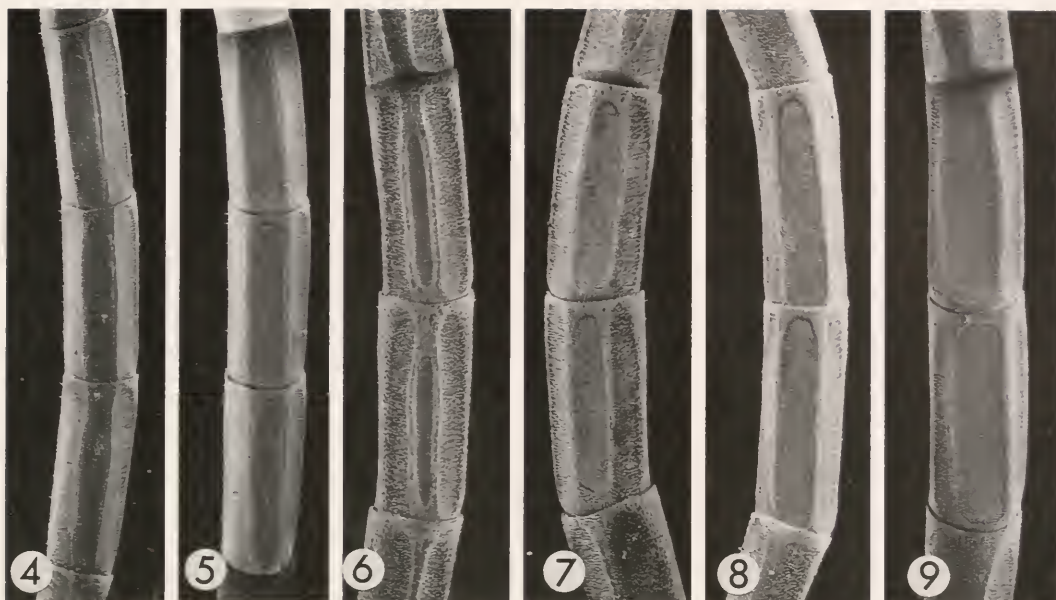
KEY TO SPECIES OF THE *SPHEX FLAVIPENNIS* GROUP
Females

- 1. Erect setae of head and thorax dark brown or black 2
- Erect setae of head and thorax white or pale yellow 4
- 2. Gaster red and black (at least tergum II partly red); foretibia(at least partly) and tarsus
amber, midtibia partly amber; wings yellow tinted with dark apical band, veins brown;
Iberian Peninsula to Greece, Slovakia, Hungary, Romania, Kazakhstan; Algeria(?)
..... *atropilosus* Kohl
- Body all black; wings darkly infumate, with no apical band 3
- 3. Appressed setae of face brown; hindfemur asetose; Iran, Turkmenistan
..... *melas* Gussakovskij
- Appressed setae of face silver; hindfemur with erect setae; northeastern Libya, northwest-
ern Egypt *libycus* de Beaumont
- 4. Petiole wider than long (as measured dorsally from base of funicle to base of tergum I) or
at least not longer than wide; Mediterranean region to central Asia *leuconotus* Brullé
- Petiole longer than wide 5
- 5. Legs black (including tarsi); gaster usually all red (sometimes bicolored or all black); east-
ern Mediterranean region to Afghanistan and Tajikistan *oxianus* Gussakovskij
- Some or all legs partly to entirely red (at least foretibia with some red apically); gaster
bicolored (all black in some areas of Kazakhstan, Siberia, China); widespread in Palearctic
Region 6
- 6. Pronotal collar and scutum with appressed white setae (best seen from in front); length
24–32 mm *flavipennis* Fabricius
- Pronotal collar and scutum without appressed white setae (scutum sometimes with nar-
row, median stripe of white setae or traces of white setae posterolaterally); length 16–26
mm *funerarius* Gussakovskij

Males

- 1. Flagellomere III with placoid 2
- Flagellomere III without placoid 4
- 2. Erect setae of head and thorax dark brown or black; flagellomeres III–VII with placoids; at
least tergum II partly red; Iberian Peninsula to Greece, Slovakia, Romania, Hungary, Ka-
zakhstan; Algeria(?) *atropilosus* Kohl
- Erect setae of head and thorax white or pale yellow; placoid distribution and gaster color
variable 3
- 3. Gaster red basally, black distally (western Palearctic; Sichuan, China), or all black (e. Ka-
zakhstan, Siberia; Gansu, China); placoids usually present on flagellomeres III–VIII (Fig.
2), but sometimes on II–VIII, II–IX, III–VI (Fig. 1), III–IX (or IV–VI in Corsica)
..... *funerarius* Gussakovskij
- Gaster all black; placoids present on flagellomeres III–VI (Fig. 3); eastern Mediterranean
region to Tajikistan and Afghanistan *oxianus* Gussakovskij
- 4. Wings nearly uniformly darkly infumate, with no apical dark band; remaining body black;
erect setae of head and thorax dark brown or black 5
- Wings nearly hyaline or yellowish to slightly infumate, with darker apical band; gaster at
least partly red; legs black or partly red; erect setae of head and thorax dark brown to pale
yellow or white 6
- 5. Iran, Turkmenistan *melas* Gussakovskij
- Northeastern Libya, northwestern Egypt *libycus* de Beaumont
- 6. Flagellomeres V–VI (Figs. 6–7) or only VI with placoids; gaster color variable
..... *flavipennis* Fabricius
- Flagellomeres IV–VI with placoids (Figs. 4–5) (Corsican *funerarius* will key here, but gaster
is red and black); gaster black *leuconotus* Brullé





Figs. 4-9. Scanning electron photographs of male antenna showing placoids on flagellomeres (= F). 4-5, *Sphex leuconotus*, 4 is specimen from Cherkas, Cyprus with placoids on F IV-VI; 5 is specimen from Zaragoza, Spain with placoids on F IV-VI. 6-7, *Sphex flavipennis*, 6 is specimen from Carpentras, France with placoids on F V-VI; 7 is specimen from Zaragoza, Spain with placoids on F V-VI. 8, *Sphex melas* from Repetek, Turkmenistan with placoids on F V-VI. 9, *Sphex libycus* from Marsa Matruh, Egypt with placoids on F V-VI.

DISCUSSION OF SPECIES

Sphex atropilosus Kohl

Sphex maxillosus var. *atropilosus* Kohl 1885:202.

Holotype: female, "Tultscha" [= Tulcea, Romania] (Wien), examined.

Sphex atrohirtus Kohl 1890:437 (lapsus for and redescription of *atropilosus*, raised to species.)

Subsequent records as *atropilosus*: Berland 1952: 88 (France); Leclercq 1955:19 (Africa); Leclercq 1956:324 (Greece); Bajári 1957:79 (Hungary); de Beaumont 1962:19 (Spain); de Beaumont 1965:14 (Greece); Pulawski 1978:183 (s. Russia, Caucasus); Mingo and Gayubo 1984: 145 (Spain); Józán 1986:367 (Hungary); Gayubo 1987:106 (Spain); Hamon, Fonfria, and Tussac 1991:131 (France); Bitsch et al., 1997: 69 (s. France); Shkuratov 1998:97 (Rostov Oblast', Russia).

Subsequent records as *atrohirtus*: Roth 1925:397

(Africa); Chaudoir 1947:142 (France); Zavalil and Šnoflák 1948:168 (Czechoslovakia); de Andrade 1949:8 (Portugal); Berland and Bernard 1949:4 (France); Hamon 1950:29 (France); Benedek 1968:70 (Hungary); Balthasar 1972:421 (Czechoslovakia); Kazenas 1978:40 (Kazakhstan); Dollfuss 1989:12, 15 (type material); Pádr (in Šedivý) 1989:166 (Slovakia).

Recognition.—The dark erect setae of the head and thorax distinguish *atropilosus* from other species in the *flavipennis* group with red and black legs and gaster. The short female petiole (at most minimally longer than wide) is similar to that of *leuconotus*, but the erect setae are pale in that species. The female mid- and hindfemora have erect setae but they are shorter on the dorsum than in *leuconotus*. The broad

←

Figs. 1-3. Scanning electron photographs of male antenna showing placoids on flagellomeres (= F). 1-2, *Sphex funerarius*, 1 is specimen from Tanger, Morocco with placoids on F III-VI; 2 is specimen from Italy with placoids on F III-VIII. 3, *Sphex oxianus* from Kondara Canyon, Tajikistan with placoids on F III-VI.

placoids on male flagellomeres III-VII differentiate *atopilosus* from *leuconotus* which has narrower ones on IV-VI (Figs. 4-5). The size range of female *atopilosus* is 18-27 mm which is somewhat less than the common parameters for females of *leuconotus* (22-33 mm).

Material examined.—Kohl's holotype bears his handwritten label "*atrohirtus* Kohl Type", and he obviously intended the species name to be *atrohirtus*, but it was published as *atopilosus*. A second female from "Transcauc." also has Kohl's label "*atrohirtus* Kohl type" (Vienna), but it was not mentioned in the original description and cannot be a type. It was listed by Kohl (1890) who also had material from Sarepta (= Volgograd, Russia).

Other material examined: SPAIN: Villarina, Salamanca, July 21, 1995 (female, Menke), Valdepeñas, June 21, 1983 (male, Menke), Madrid (female, CAS); FRANCE: Canet, June 14, 1948 (female, Menke), St. Nazaire, June 14, 1948 (male, Menke); GREECE: Kalamata (one of a series studied by de Beaumont 1965) (male, CAS); RUSSIA, Kalmyk Republic: 10 km NW of Chernozemel'sk (female, CAS); and ALGERIA: "Oran, 1895", collected by Schmiedeknecht (three females, one male, Vienna) and identified by Kohl as "*atrohirtus*" (i.e., *atopilosus*). However, these Algerian specimens may have incorrect provenance labels (see Distribution below).

Holotype features.—Kohl's holotype has yellow tinted wings. The legs are largely black but the following are reddish: anterior face of forefemur, and all of foretibia and tarsus; distal fourth of anterior face of midfemur, and anterior face of midtibia. Tergum I is red but there is a large, circular black spot on the anterior face. Tergum II is entirely red, and III is red laterally. Sterna I-III are red (except petiole is black). The specimen is 21 mm long.

Variation.—Petiole length and color of the gaster and legs vary in *atopilosus*. Female petiole length varies from $0.9\times$ to

$1.1\times$ its apical width, but it is usually slightly more than the distal width (example ratios are 18:17, 19.5:17, 21:20). Sometimes the dimensions are equal. In the largest female studied, a specimen 27 mm long labeled Oran, the petiole is slightly shorter than its width (ratio 21:24). In smaller specimens from Oran the petiole is as long as wide. Increasing body size thus may be correlated with a shortening of the petiole. The male petiole is longer than wide (20.5:17.5, Oran; 20:14, Greece).

Gaster color in the female from Chernozemel'sk is similar to the holotype, but the red is limited to tergum I apically and laterally and tergum III basolaterally. Red is reduced in the Spanish females: narrow strip along distal margin of tergum I, tergum II laterally, and most of sternum II. The Spanish male is similar, but additionally has red laterally at the extreme base of tergum III (M. Ohl *in litt.* to Menke says tergum III is all black in Spanish males he has studied). A female and male from France are similar, but the red is more extensive in the female: tergum II all red, and III red basolaterally. In the Greek male red covers the sides of tergum I, all of II, tergum III basolaterally, all of sternum II, and the basal half or so of sternum III.

Legs are bicolored in females, but the amount of black and red varies. The female from Russia is similar to the holotype, but the posterior surface of the foretibia is black. The midleg of one female from Oran is black except for a small, circular amber spot at the femoral apex, and the hind surfaces of the foreleg are dark. In the Spanish females red is limited to the apex of the fore- and midfemora anteriorly, and to the anterior surfaces of the fore- and midtibiae. The legs are all black in the French and Greek males.

Females are 18-27 mm, and males are 17-22 mm long.

Distribution.—Northern Mediterranean region (except Italy) eastward to Kazakh-

tan. The species is uncommonly collected, although locally abundant at times.

Specimens mentioned above labeled Oran, Algeria, may have been mislabeled since the species has not been collected in that country by modern workers (e.g., de Beaumont, Guichard, Roth); nor did collectors of the 1890's find it (Saunders 1910, Morice 1911). The only other record from Algeria is by Roth (1925) who saw a female from Orléansville (now El Asnama) dated 1867 in the Sichel Collection (Paris).

***Sphex flavipennis* Fabricius**
(Figs. 6–7)

Sphex flavipennis Fabricius 1793:201. Lectotype: female, "Italia" (Copenhagen), designated by van der Vecht 1961:31, not examined.

Sphex rufocinctus Brullé 1833:367. Holotype (or syntype): male, "Pétalidi, Morée" [= Korone or Koroni, Peloponnesus, Greece] (Paris), examined. **New synonym.**

Sphex bicolor Dahlbom 1845:437. Holotype: male, "Dalmatia" [= coastal Croatia and Montenegro] (Berlin?), (junior primary homonym of *Sphex bicolor* Fabricius 1775), not examined. Synonymy by Kohl 1881:39 who saw Dahlbom's material (with *maxillosus*), and Kohl 1890:236 (with *flavipennis*).

Sphex cinereorufocinctus Dahlbom 1845:437. Syn-types: male, "Rhodus" [= Rhodes, Greece] (Lund), not examined. Synonymy by de Beaumont 1949:127 who saw Dahlbom's material.

Sphex sellae Gribodo 1873:86. Holotype: female, "Sicilia" [= Sicily, Italy] (Genova?), not examined. Synonymy by Kohl 1890:236.

Sphex flavipennis var. *rufodorsatus* De-Stefani 1887:88, pl. 2, fig. 8. Holotype: female, "Sicilia" [= Sicily, Italy] (Palermo?, Genova?, destroyed?), not examined. Synonymy by Kohl 1890:236.

Recognition.—The presence in most females of appressed white setae on the pronotal collar and scutum identifies *flavipennis* and separates the species from the similar *funerarius* which lacks such pubescence. Unfortunately the appressed setae are poorly developed in some populations, and in older material they are often

worn away. In such cases association with males may offer the only reliable means of identification (note however, that if long, erect setae are present but appressed setae are absent, it is likely that a specimen is not *flavipennis*). Females of *flavipennis* tend to be larger than those of *funerarius* (24–32 mm long versus 16–26 mm). Some females of *Sphex leuconotus* have appressed white setae on the thoracic dorsum but the petiole is shorter than wide or at most as long as wide. Females of *flavipennis* have a petiole that is longer than wide.

The appressed pale setae are less developed in males, but placoids are found only on flagellomeres V–VI (rarely only on VI), and they are narrow (Figs. 6–7). In *funerarius*, placoids are broad (Figs. 1–2) and usually present on flagellomeres III–VIII (but see that species for placoid variation). Males of *leuconotus* have placoids on flagellomeres IV–VI (Figs. 4–5).

Females are 24–32 mm, and males are 17–26 mm long.

Previous workers have used other characters to identify *flavipennis*, but we have found them unreliable: yellow-tinted wings and golden erect setae on the face. The erect facial setae are sometimes silver in *flavipennis*, and nearly always this color in *funerarius*. The yellow tinted wings, from which the species derives its name, is not a reliable recognition character for *flavipennis* because some *funerarius* also have yellowish wings, although typically they are lightly brown stained. Several authors have used comparative lengths of the petiole and hindtarsomere I or III to distinguish females of *flavipennis* from *funerarius*. It is unclear how petiole length was measured by these workers, but we have been unable to find any useful differences. Comparisons of the length and width of the female petiole itself show nearly the same parameters in both species (15 specimens of each species measured): *flavipennis*—petiole length is 1.1 to 1.4× width; *funerarius*—petiole length is 1.1 to 1.6× length.

Hamon, Fonfria, and Tussac (1991) illustrated two male characters that earlier authors had used to separate *flavipennis* and *funerarius*: the form of the clypeal free margin and the length of the lateral setal brushes of sternum VII. These characters are useful, but they are not always reliable. The clypeal free margin in *flavipennis* is usually a simple arc, but sometimes there is a shallow emargination that may be broad or narrow. In *funerarius* the clypeal free margin usually has a pronounced emargination (see Fig. 10 in Hamon et al. 1991). The lateral setal brushes of male sternum VII are shorter in *flavipennis* in comparison to *funerarius* (see figs. 11–12 in Hamon et al. 1991), but the reliability of this character remains to be proven.

Type material.—Brullé's holotype (or sole surviving syntype) of *rufocinctus*, a male, has been studied by each of us on two occasions. The specimen is poorly preserved, very dirty, and badly worn. The mandibles are truncated from considerable use, and the setation of the clypeal disk is worn away. The type has lost most of its antennae; the scapes and pedicels remain, and the right antenna still has flagellomeres I–II. Although the pronotum is dirty, some silver appressed setae (one of the characteristics of *flavipennis*) are faintly visible. Traces of appressed silver setae are also visible in the scutal furrows and on the hindmargin of the scutellum. The clypeal margin is not emarginate although it is straight at the middle. The lateral setal brushes on sternum VII are dirty, but the setae are as short as in *flavipennis* (shorter than in *funerarius*). The body length of 25 mm is also typical of male *flavipennis*. The gaster is mostly black, but tergum II is red except for a narrow, transverse dark band along the distal margin, and tergum III is red laterally. This color pattern is typical of *flavipennis*. These characters convince us that the type of *rufocinctus* is not conspecific with *funerarius* (*maxillosus* of authors), but instead is *flavipennis* Fabricius. The bi-

colored gaster indicates that *rufocinctus* is not conspecific with *leuconotus*.

We have been unsuccessful in locating the type material of *bicolor* Dahlbom, *sellae* Gribodo, and *rufodorsatus* De-Stefani, and have relied on Kohl (1890) for their synonymy.

Variation.—Occasionally the thoracic dorsum of female *flavipennis* has reddish areas, a trait that immediately identifies Mediterranean specimens as this species (similar reddish areas are found on some central Asian specimens of *funerarius*). De Beaumont and Bytinski-Salz (1955) noted that occasional Israeli females have an entirely red thorax, but they occur with normally colored specimens. The thorax of some females in Iran is also extensively red (de Beaumont 1957). De Beaumont (1960) noted a male from Cyprus with a placoid only on flagellomere VI.

In a male of *flavipennis* from the Mashad area, Iran (CAS), the lateral setal brushes of SVII are longer than a midocellus diameter. Four other males from Mashad have typically short brushes.

Distribution.—Mediterranean region including islands of Mallorca, Sardinia, Sicily, Crete, Rhodes and Cyprus; eastward to Hungary, Bulgaria, and south-central Asia (Kazakhstan, Uzbekistan, Tajikistan, Turkmenistan); Arabia: United Arab Emirates; Iran, Afghanistan.

Sphex funerarius Gussakovskij

(= *Sphex maxillosus* of authors before 1976, or *rufocinctus* of authors after 1975) (Figs. 1–2)

Sphex maxillosus Fabricius 1793:208. Lectotype: female, "Barbaria" [= northwest Africa] (Copenhagen), designated by van der Vecht 1961:30, (junior primary homonym of *Sphex maxillosus* Poiret 1787).

Sphex obscurus Fischer de Waldheim 1843:122. Syntypes: male, "in Rossia australi" (Moscow, St. Petersburg, Dresden?), (junior primary homonym of *Sphex obscurus* Schrank 1802, and *Sphex obscurus* Fabricius 1804). Synonymy with *maxillosus* by Kohl 1895:69. **New synonym.**

Sphex maxillosus var. *pedibus nigris* Zanon 1925: 90. Holotype: female, Fueihat, Libya (Genova?). Polynomial, not available, see Art. 11.4 of the Code.

Sphex funerarius Gussakovskij 1934:3. Lectotype: male, [Bei-lung-shui,] S. Kansu [= Gansu], China (Stockholm), **here designated** in order to ensure the name's proper and consistent application, examined. **New synonym.**

Sphex maxillosus ssp. *mavromoustakisi* de Beaumont 1947:383. Holotype: female, Polemidia Hills, Cyprus (Lausanne), examined. **New synonym.**

Sphex rufocinctus (misinterpretations since 1975): Lomholdt 1975:68 (Gotland I., Sweden); Bohart and Menke 1976:116 (listed, nomenclature problems); Guichard 1978:270 (Greece); Richards 1979:400 (British Channel Is.); Pagliano 1980:110 (Italy); Dollfuss 1983:2 (Austria); Mingo and Gayubo 1984:146 (Spain); Schmidt and Westrich 1983:120 (Greece); Gayubo 1984:356 (Portugal); Gayubo and Tormos 1984:8 (Spain); Pagliano 1984:367 (Italy); Chevin and Chevin 1985:38 (France); Eiroa and Novoa 1985:23 (Spain); Józán 1985:55 (Hungary), 76 (floral records), 83 (ecological and zoogeographic characteristics); Pagliano 1985:12 (Italy); Tormos and Jiménez 1985:32 (Spain); Westrich and Schmidt 1985b:112 (Germany: endangered in Baden-Württemberg); Gayubo 1986a:35 (Spain), 1986b:30 (Spain); Gayubo and Heras 1986:26 (Spain); Gayubo and Sanza 1986:27 (Spain); Gayubo and Tormos 1986a:8 (Spain), 1986b:4 (Spain); Islamov 1986:515 (Uzbekistan); Asís and Jiménez 1987:23 (Spain); Gayubo 1987:106 (Spain); Tormos and Jiménez 1987a:122 (Spain), 1987b:316 (Spain); Andersson et al. 1987:72 (endangered in Sweden); Dollfuss 1987:18 (latest Austrian specimens collected in 1952 and 1953); Schmidt and Westrich 1987:358 (Germany); Chevin 1988:14 (France); Dollfuss 1988:20 (Austria); Janzon 1988:1 (Sweden); Karsai 1988:99 (Hungary); Islamov 1989:49 (Uzbekistan: nest and prey); Jacobs 1989:3 (Germany); Józán 1989:100 (Hungary); Asís, Gayubo, and Tormos 1990:240 (mature larva); Gayubo, Asís, and Tormos 1990:9 (Spain); Jacobs and Oehlke 1990:122, 132 (German Democratic Republic: not collected after 1960); Pagliano 1990:60 (in catalogue of Italian Sphecidae); Day 1991:xix (summary of European Endangered Hyme-

noptera Lists); Dollfuss 1991:27 (in revision of Austrian Sphecidae); Gayubo, Borsato, and Osella 1991:392 (Italy); Gayubo and Torres 1991:Table I and p. 81 (Spain: effects of urban pressure); Hamon, Fonfria, and Tussac 1991:128, 131 (in key to French Sphecini), 132 (France); Józán 1991:602 (Hungary); Kazenas and Nasyrova 1991:38 (Kazakhstan); Negrisolo 1991:316 (Italy); Schembri 1991:177 (previous records from Malta); Gayubo, Borsato, and Osella 1992:275 (Greece, Turkey); Józán 1992:171 (Hungary); Kazenas and Tobias 1992:29 (sleeping aggregations); Gayubo, Tormos, and Asís 1993:308 (teratological specimen); Torregrosa, Gayubo, Tormos, and Asís 1993:11 (Spain); Luchetti 1993:10 (Italy: Sardegna); Dollfuss 1994:98 (endangered in Austria); Gayubo and Borsato 1994:199 (Italy); Tormos, Asís, and Gayubo 1994:187 (Spain); Józán 1995:104 (Hungary); Krasnobayev et al. 1995:139 (Russia: Samara Oblast'); Negrisolo 1995:18, 22 (floral records); Pagliano and Pesarini 1995:83 (Italy); Pagliano and Scaramozzino 1995:731 (Italy); Schmid-Egger, Risch and Niehuis 1995:208 (Germany); Vernier 1995:176 (in key); Gusenleitner 1996a:809 (Austria), 1996b:818 (Croatia); Minoranskiy and Shkuratov 1996:81 (Russia: Rostov Oblast'); Schmid-Egger 1996:19 (Germany); Schmid-Egger, Schmidt, and Doczkal 1996:374, 378 (Germany: endangered); Voblenko, Gorobchishin and Nesterov 1996:14 (Ukraine); Bitsch et al. 1997:71 (in sphecid fauna of western Europe); Schmidt and Schmid-Egger 1997:27 (in checklist of German Sphecidae); Dollfuss, Gusenleitner, and Bregant 1998:509 (Austria); González, Gayubo, and Torres 1998:72, 73 (Spain); Zehnder and Zettel 1999:13 (Switzerland); González, Gayubo, and Torres 1999:334.

Recognition.—*Sphex funerarius* varies over its extensive range, both in female and male color and number of male antennal placoids. Some females especially can be difficult to separate from *oxianus* and *flavipennis*. Males are easiest to identify because most specimens have broad placoids on flagellomeres III-VIII (Fig. 2) (males from Corsica are among the more notable exceptions—see Variation below). Only two other species have a placoid on

III: *atropilosus* and *oxianus*. However, the erect setae on the head and thorax are white or pale yellow in male *funerarius*, while they are dark brown or black in *atropilosus*. Most commonly males of *funerarius* have a bicolored gaster in contrast to the all black gaster of *oxianus*. Males of *funerarius* from China can have a black gaster, but the presence of placoids on flagellomeres III-VIII will separate them from *oxianus* which has placoids only on III-VI (Fig. 3) and is unknown from China.

The following are variable in the species, but may aid in identification. The male clypeal free margin usually has a pronounced broad emargination in *funerarius*, and is arcuate or shallowly emarginate in *flavipennis*. However, exceptions in both species weaken the usefulness of this difference. The lateral setal brushness on male sternum VII are longer than a midocellus diameter in *funerarius*, while in other species these are usually shorter than, or about equal to a midocellus diameter. However, there are also exceptions to this character (see Variation under *flavipennis*).

The absence of appressed pale setae on the pronotal collar and scutum separates females of *funerarius* from *flavipennis*. Females of *flavipennis* typically have appressed silver setae on the thorax, but this pubescence is often sparse or worn away. Thus, association with males is often the best way to identify females of both species. As noted under *flavipennis*, female petiole length is essentially identical between the two species. Females of *funerarius* usually have bicolored fore- and midlegs, and the hindleg, except for the tarsus, is usually black. However, red is limited to the foretibial apex in some melanistic Chinese specimens. A similar leg pattern is present in one Iranian female seen by us, but, unlike the black Chinese specimens, the gaster is bicolored. Females of *oxianus* have entirely black legs, including the tarsi.

Females are 16–26 mm, and males are 17–20 mm long.

Nomenclatural history.—This relatively common Palearctic species was known as *Sphex maxillosus* Fabricius 1793, for more than 170 years. Then van der Vecht (1959: 214) pointed out that Fabricius' name was a junior homonym of *Sphex maxillosus* Poiret 1787, currently assigned to the genus *Chlorion*. He noted that unless Poiret's name was suppressed, *maxillosus* Fabricius would have to be replaced by the next available synonym. Van der Vecht believed that to be *leuconotus* Brullé based upon Dalla Torre's (1897) catalog, but that is not true. Bohart and Menke (1976:116) called the species *rufocinctus* Brullé 1833, adopting the first of several synonyms of *maxillosus* recognized by Kohl (1890:433), even though Menke pointed out (footnote 23) that the type of *rufocinctus* appeared to be a synonym of a different species, *flavipennis* Fabricius. Menke urged European workers to study the problem and clarify the identity of Brullé's species. That action has not been forthcoming, and, unfortunately, nearly all contemporary authors since 1976 have used *rufocinctus* as the proper name for the invalid *maxillosus* Fabricius. Our studies of the Brullé types establishes that none of his names, *rufocinctus*, *leuconotus*, or *triangulum*, are available for *maxillosus* Fabricius. Instead, the oldest available name is *funerarius* Gussakovskij 1934.

Type material.—Gussakovskij (1934) listed 15 males and 3 females of *funerarius* from Bei-lung-shi, S. Kansu, China, 15-VI-30, and 2 males from N. O. Szechuan, China, 20-V-30, all collected by Dr. Hummel, and also 3 males and a female from southern Altai (Karasengir) [= Siberia], and one male from Saissan [= Lake Zaisan, Kazakhstan]. We have examined three male and six female syntypes (Stockholm). All but one male are labeled Kina [= China], S. Kansu, Sven Hedins Exp. Ctr. Asien, Dr. Hummel, and one male and one female from Kansu have Gussakovskij's species labels with the word "typus". One male is labeled Kina, N. O. Szechuan, etc., and

it also has a Gussakovskij label. We have selected and labeled as lectotype the male from S. Kansu with Gussakovskij's "typus" label. We have also put paralectotype labels on the male and female that have Gussakovskij labels. The three males have placoids on flagellomeres III-VIII and are entirely black. The females are black except the apical half of the foretibia which is brownish red. In one female the whole outer side of the foretibia is reddish. In two females the inner apex of the forefemur is also reddish.

Variation in placoid distribution.—In a series of papers de Beaumont (1960:229; 1961a:272; 1961b:45; 1967:276; 1970b:4) studied variation in the number of placoids in western Palearctic males. He recorded their distribution as follows: on flagellomeres III-VIII (most European specimens, Fig. 2), but occasionally II-VIII or III-VII; II-VIII or II-IX (Turkey); II-VIII (Crete, Iran); II-IX (Afghanistan); II-VIII or II-IX (Cyprus); and III-VI (Fig. 1), III-VII, or III-VIII (north Africa). Males from the island of Corsica are exceptional in lacking placoids on flagellomeres II and III (de Beaumont 1960:229, also one male in CAS). On this island placoids are only found on flagellomeres IV-VI, and we suspect this to be the typical condition on that island.

Color variation and subspecies.—Female legs are bicolored throughout the range of *funerarius*, although the hindleg is often largely black. The following are commonly red: tibiae and tarsi of the fore- and midlegs and the hindtarsi (the midtibia varies from all red to partially or wholly black). Sometimes the fore- and mid-femora have red areas distally. However, the legs are almost wholly black in females from Gansu, China (type series of *funerarius*) except for some reddish brown on the forefemoral apex and inner side of the foretibia. In one specimen of this series red occurs only on the inner apical half of the foretibia. Specimens that we have seen from other parts of China display the typ-

ical color pattern of the species. Intermediate leg color patterns are seen in four females from Iran (CAS): the foretibia is black and red, and the midleg is all black except for an inner distal red spot on the femur, and the tarsi are sometimes brownish (Elburz Mts.); or the foretibia is black and red and the midtibia is reddish on its anterior surface only, and the midtarsus is brownish (Khorasan). Another Iranian female from Tilabad (USNM) has entirely black legs except for red on the anterior surface of the foretibia.

In females of most populations of *funerarius*, the gaster is red with a black apex (segments IV-VI or V-VI typically). However, the gaster may be all black in females from eastern Kazakhstan, southern Siberia, and the provinces of Sichuan and Gansu in China (sternum II pale laterally in some specimens from Gansu). The gaster is also all black in males from Siberia and Gansu, China. In females from Cyprus, the gaster (except the black petiole), femora and tibiae are red. This insular population was described as *maxillosus mavromoustakisi* by de Beaumont (1947). We have examined the type series of *mavromoustakisi* (2 females, 3 males, from Cyprus), and do not feel that recognizing the subspecies is warranted. The Corsican population, for example, is as distinct based upon male antennal placoid distribution, and yet we also feel it needs no name.

The thorax is typically all black in *funerarius*, but it is partly red in a female from the Kopet-Dagh Mountains south of Ashkhabad, Turkmenistan (CAS). The following are red in this specimen: pronotum apicomeresally and laterally, most of scutum, scutellum, postscutellum and part of propodeal dorsum. Additionally only the last gastral segment (VI) is black in this specimen, and the inner side of the hindtibia is reddish.

Larva.—The mature larva of *funerarius* was described by Asís, Gayubo, and Tormos (1990).

Conservation.—*Sphex funerarius* was list-

ed as endangered in Austria, Germany, and Sweden (summary in Day 1991, also Andersson et al. 1987, and Janzon 1988). Dollfuss (1987) reported that the last Austrian specimens were collected in 1952 and 1953, and Jacobs and Oehlke (1990) noted that no specimens were collected in the former German Democratic Republic after 1960. One female, however, was found in Austria in 1996 (Gusenleitner 1996a). Schmid-Egger, Risch, and Niehuis (1995) reported that the species was relatively common in the upper Rhine area of Germany in the 1950's and early 1960's, but disappeared subsequently. However, sightings of *funerarius* increased in the states of Hessen, Baden-Württemberg, and Rheinland-Palatinate. M. Ohl in litt. to Menke says the species has also been found recently in Bavaria. Janzon (1988) noted that on the Swedish island of Gotland *funerarius* occurs in open sandy areas, often along the shore. Habitat overgrowth is the main danger to populations of *funerarius* on this Baltic island.

Distribution.—Mediterranean Basin including North Africa from Morocco to Egypt. The Balearic Islands (Compte Sart 1959), as well as the islands of Corsica, Sardinia, Sicily, Malta, Crete, and Cyprus. Recorded from Jersey in the Channel Is. (Richards 1979), but the species does not occur on the British Isles proper. Most of Europe north to Gotland I. and Fårö I. in the Baltic Sea but not in Sweden proper (Andersson et al. 1987) and Poland; eastward to Hungary, Romania, Bulgaria, s. Russia, Siberia (Krasnoyarsk), and south-central Asia: Iran, Afghanistan, Uzbekistan, Kazakhstan, Turkmenistan, Tajikistan; n. China (Gansu, Sichuan, Nei Mongol, Shandong, Liaoning).

***Sphex leuconotus* Brullé, new status**

(*Sphex afer* of authors)

(Figs. 4–5)

Sphex leuconotus Brullé 1833:366. Holotype: female, "Pétalidi, Morée" [= Korone or Koroni, Peloponnesus], Greece. (originally Par-

is, now lost). Neotype: holotype of *Sphex triangulum* Brullé, **present designation** in order to ensure the name's proper and consistent use (Paris), examined.

Sphex triangulum Brullé 1833:365, pl. 50, fig. 6. Holotype: female, "Pétalidi, Morée" [= Korone or Koroni, Peloponnesus], "à la fin de Mai", Greece (Paris), (junior primary homonym of *Sphex triangulum* Villers 1789), examined. **New synonym.**

Sphex afer Lepeletier 1845:350. Lectotype: female, Oran, Algeria, designated by Menke in Bohart and Menke 1976:114 (Paris). **New synonym.**

Sphex sordidus Dahlbom 1845:436. Syntypes: sex unknown, "Rhodus" [= Rhodes, Greece] (Stockholm?). Regarded as subspecies of *afer* by de Beaumont 1953:195. **New synonym.**

Sphex tristis Kohl 1885:200. Syntypes: male, Spain (Wien). Synonymy with *afer* ssp. *sordidus* by de Beaumont 1953:105. **New synonym.**

Sphex plumipes Radoszkowski 1886:25, figs. 18a-i. Holotype: male, Askhabad [Turkmenistan] (Kraków), (junior primary homonym of *Sphex plumipes* Drury 1773), examined. **New synonym.**

Sphex pachysoma Kohl 1890:436. Syntypes: female, "Kilasi" and "Kuba Breku" [= Kilyazi and Kuba, Azerbaijan?]; Cyprus; "Syra" [= Syros I., Greece] (Wien). Synonymy with *tristis* by Dusmet and Mercet 1906:516, with *afer* by Schulz 1911:68 and with *afer* ssp. *sordidus* by de Beaumont 1953:195. **New synonym.**

Recognition.—The female and most males of *leuconotus* can be recognized by an unusually short petiole whose distal width is usually greater than the length. In occasional specimens the measurements are equal. In 12 females measured, the petiole width varied from 1.0× to 1.5× its length, with the average being 1.2×. Some females have appressed white setae on top of the pronotal collar. Traces of appressed white setae can also sometimes be seen on the scutum. In the male, narrow placoids are present on flagellomeres IV–VI (Figs. 4–5).

Females are 25–34 mm, and males are 17–23 mm long.

Type material and synonymy.—Kohl

(1890:433) synonymized *triangulum* Brullé with *Sphex maxillosus* Fabricius, and Bohart and Menke (1976) listed it as a synonym of *rufocinctus* Brullé. The holotype (or the only surviving syntype) is actually identical with *Sphex afer sordidus* Dahlbom. The specimen has the typical short petiole of *afer* (ratio 24:19). The mid and hindfemora have long, erect setae on the upper, outer, and lower surfaces. Tergum I of the type is mostly black (apex red), and terga IV-VI are also black. Terga II-III are red. The legs are black and the wings are yellowish. The name *triangulum* Brullé is a junior homonym.

The next available name for this species is *leuconotus* Brullé which was collected at the same locality as *triangulum*. We were unable to find a type of *leuconotus* in Paris, and apparently it has been destroyed. Brullé stated that *leuconotus* and *triangulum* were very similar, differing primarily in the form of the mandible and the setation of the clypeus. His description of the mandible of *triangulum* suggests that he had a female with mandibular wear common to old specimens, the result of much nest excavation, and this is confirmed by examination of the holotype. The mandibles are badly worn. Concurrent with such wear is the loss of clypeal setation, and Brullé described the clypeus of *triangulum* as being largely devoid of setae. Brullé's specimen of *leuconotus*, on the other hand, must have been a fresh one, judging from his description. The mandible was long, and the clypeus was mostly covered with setae. In his description of *leuconotus*, Brullé referred to plate 14, fig. 1, in Savigny's (1809-1829) *Description de l'Egypte*. The figures on the plates from this work are remarkable for their time, but they were based on material from Egypt, and *Sphex afer* is not known from that country. The wasp shown in figure 1 has a short petiole although it is longer than wide. The accompanying figure of the mandible shows an unworn one with a long, acuminate apex. Perhaps Brullé simply wanted to in-

dicate that his *leuconotus* was similar to Savigny's figure. In any case, his description of *leuconotus* agrees with *afer sordidus*.

Since the differences between *leuconotus* and *triangulum* appear to represent age differences of the specimens, and Brullé's own feeling was that he would otherwise regard them as identical, we are certain that *leuconotus* is conspecific with *triangulum*. Accordingly we have made the type of *triangulum* the neotype of *leuconotus* and have so labeled it.

A result of the foregoing is that *Sphex afer sordidus* must now be called *leuconotus* Brullé. According to de Beaumont (1953: 195), *tristis* Kohl and *pachysoma* Kohl are synonyms of *sordidus*. Thus they are new synonyms of *leuconotus* Brullé s.s.

We have also studied the male type of *plumipes* Radoszkowski. It is labeled "plumosus" in Radoszkowski's handwriting, and agrees with his description, but the type lacks its antennae and the gastral apex, presumably lost when he extracted the genitalia (which are glued to a piece of card mounted on the pin with the specimen). *Sphex plumipes* was tentatively synonymized with *pachysoma* (i.e., *leuconotus*) by Kohl (1890:436), whose interpretation is most likely correct. The type is all black with some appressed white setae on the collar, almost silvery scutal setae, and slightly yellowish wings with a darker apical band. This color combination is found only in *leuconotus* and *oxianus*, but the holotype's relatively short gastral petiole (length equal to 1.25× apical width) suggests *leuconotus*. In any case, Radoszkowski's name is a junior homonym.

Color variation and subspecies.—Gaster color varies in females. Sometimes it is entirely red (Cyprus, Uzbekistan), or tergum I may be black basally and IV-VI entirely so (Cyprus, Spain, n.w. Africa). In Romania the gaster may be all black (Scobiola 1960), and de Beaumont (1960:227) studied a single female with a black gaster from eastern Libya and four females with bicolored gasters from western Libya.

Males of *leuconotus* from northwest Africa have darker erect body setae than specimens from the northern Mediterranean and eastward, and the wings are smoky. The wings are clear in the eastern Libyan female mentioned above, and those from western Libya are less smoky than females from northwest Africa. Those who would like to treat the northwest African population as a subspecies (an action we do not endorse) will have to call it *leuconotus* ssp. *afer*.

Distribution.—Mediterranean region (except Egypt and known only from the Pyrénées-Orientales Département in France) including islands of Sardinia, Rhodes, and Cyprus; eastward to Bulgaria, Greece, Turkey, Israel, Iraq, Iran, Afghanistan and the central Asian republics of Kazakhstan, Turkmenistan and Uzbekistan.

***Sphex libycus* de Beaumont**

(Fig. 9)

Sphex libycus de Beaumont 1956:182. Holotype: female, Porto Bardia, Libya (Zürich), not examined. Subsequent record: de Beaumont 1960:227 (Libya, Egypt).

Recognition and status.—This species is wholly black except for appressed silver facial setae in both sexes. The wings are darkly infumate. The female hindfemur has erect setae, and the male has placoids on flagellomeres V-VI (Fig. 9). *Sphex libycus* is almost identical to *melas* Gussakovskij, another all black species, and certainly the males cannot presently be separated. The only difference in the females is the color of the appressed facial setae: silvery in *libycus* and brown in *melas*. Erect hindfemoral setae are present on the posteroventral edge in *libycus*, but in *melas* they may be present (Iranian female) or absent (Turkmen female). Much more material of both species is needed to determine if *libycus* is a valid species or merely a geographic color form of *melas*.

Females are 24–28 mm, and males are 20–22 mm long.

Taxonomic history.—*Sphex libycus* was first described in detail by Roth (in Schulthess 1926:210) who studied one female from Agedabia in Cyrenaica, Libya, calling it "*Sphex maxillosus* var. *tota nigra*, *alis valde infumatis*." He noted the all black body (except for partly dark red mandibles), the dark body setation, and intensely infumate wings. De Beaumont (1956) recognized that Roth's wasp was a different species and gave it the name *libycus*.

Material examined.—We have seen three females and four males collected 64 km W of Marsa Matruh, EGYPT, by Pulawski on 28–29 May 1993 (CAS, USNM).

Distribution.—Known only from the northeast coast of Africa: northeastern Libya and northwestern Egypt.

***Sphex melas* Gussakovskij**

(Fig. 8)

Sphex melas Gussakovskij 1930:207. Syntypes: male, female, Repetek, Turkmenistan (St. Petersburg), not examined.

Recognition.—*Sphex melas* is nearly unique in the *flavipennis* group in being all black, including the wings, legs, and all erect setae. Appressed silver setae are found only on the face of the male. *Sphex libycus* is the only similar species, but the brown appressed facial setae of female *melas* separate it from *libycus* which has silver facial setae. Males of the two species cannot presently be separated morphologically. Other characters of *melas* include: no silvery setae on pronotum, male with broad placoids on flagellomeres V-VI (Fig. 8, placoids narrower in *flavipennis* Figs. 6–7), and lateral setal brushes of sternum VII markedly shorter than in *funerarius*.

Females are 22–28 mm, and males are 15.5–17 mm long.

Some male specimens of *Sphex funerarius* from the eastern part of its range (e. Kazakhstan, s. Siberia, China) are all black, as are males of *oxianus* and some males of *leuconotus*. However, the erect body setae are pale in these species, and the wings are only slightly infumate.

Material examined.—We have examined topotypic material of *melas* (2 females, 4 males) determined by Gussakovskij (Moscow, CAS, USNM), and also a female from Hamadan, IRAN (CAS) and a female from Imam Baba, TURKMENISTAN (USNM).

Distribution.—Turkmenistan and Iran.

***Sphex oxianus* Gussakovskij**
(Fig. 3)

Sphex oxianus Gussakovskij 1928:3. Syntypes: male, "Kara-tau mountains, right shore of Amu-Darya, below Khiva" [Uzbekistan] (St. Petersburg), not examined. Subsequent records: Gussakovskij 1930:208 (description of female; Turkmenistan, Uzbekistan); Gussakovskij 1933:273 (Iran); Gussakovskij 1935:413 (Tadjikistan); de Beaumont 1960:170 (Afghanistan); de Beaumont 1967:276 (Turkey); de Beaumont 1968:156 (redescription); de Beaumont 1969:81 (Turkey); de Beaumont 1970a:393 (Afghanistan); de Beaumont 1970b:4 (Iran).

Sphex oxianus form *nubilus* de Beaumont 1968:156. Holotype: female, Ein Gedi, Israel (W. Schlaffle Collection, Kaiseraugst, Switzerland), not examined. Bohart and Menke (1976:116) listed *nubilus* as a subspecies of *oxianus* thus validating de Beaumont's name—Article 45.6.4.1 of the Code, 4th edition (ICZN, 1999). **New synonym.**

Recognition.—The entirely black legs, including the tarsi, separates *oxianus* from other species in the *flavipennis* group except *melas* and *libycus* which are similarly colored. However, *oxianus* has pale erect setae on the head and thorax, unlike the dark setation of *melas* and *libycus*. The female petiole is longer (length $1.6\text{--}2.0 \times$ width) than in the other species of the group. For example: $0.6\text{--}1.0 \times$ apical width in *leuconotus*, $0.9\text{--}1.1 \times$ apical width in *atropilosus*, $1.1\text{--}1.4 \times$ apical width in *flavipennis*, and $1.1\text{--}1.6 \times$ apical width in *funerarius*. In the male, broad placoids are present on flagellomeres III–VI (Fig. 3), the gaster is all black, and the lateral setal brushes of sternum VII are inconspicuous (shorter than in *funerarius*).

Females of *oxianus* from the eastern

Mediterranean with an all black gaster can be distinguished from the similarly colored *melas* by the pale erect body setae. Most females of *oxianus* have virtually no erect setae on the mid- and hindfemora, or setation is very sparse. In contrast, females of *flavipennis* and *funerarius* usually have some erect setae on the mid- and hindfemora, especially on the lower surface. The femora of female *leuconotus* have considerable erect setae.

Diagnostic characters given by Gussakovskij (1928, 1930) are of little value because he compared the species to *Sphex pruinosus* Germar rather than to a species in the *flavipennis* group. De Beaumont (1968) thought that *oxianus* differed from *flavipennis* and *funerarius* (as *maxillosus*) in being slenderer, in having a slightly longer female petiole, finer body sculpture, and a female clypeus that is smooth and shiny along the median line and next to the clypeal lip. However, only the female petiole length is useful.

Females are 19–29 mm and males are 14.5–22 mm long.

Material examined.—We have seen a male and female identified by Gussakovskij as *oxianus* from TADJIKISTAN: Changuir and Kabadian (Menke, USNM), and one female identified by Gussakovskij from TURKMENISTAN: Krasnovodsk (Menke). The following have also been studied, all in the CAS: TURKEY: Urfa (male, female); TURKMENISTAN: Baharden (3 females); TADJIKISTAN: Ramit, Dushanbe, Khodzha, and Kondara Canyon (3 males, 4 females).

Variation.—Both Gussakovskij and de Beaumont thought the female was characterized by an entirely red gaster (excluding the petiole), although de Beaumont saw an all black specimen from Israel (his *nubilus*). De Beaumont (1969:81) noted a female from Turkey in which gastral segments V–VI were black, the remainder red. We have seen similar females from Urfa, Turkey, and Baharden, Turkmenistan (all CAS). The gaster and petiole are all red in

a female from Dushanbe, Tajikistan (CAS). From this we conclude that the female gaster varies from all red to all black in *oxianus*.

Distribution.—Israel, Turkey, Iran, Afghanistan, Uzbekistan, Turkmenistan, and Tajikistan.

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***Didineis massaica*, New Species, the First Afrotropical Member of the Genus, and Redescription of *Didineis nigricans* Morice, 1911 (Hymenoptera: Apoidea: Crabronidae: Bembicinae)**

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Abstract.—*Didineis massaica* Pulawski, new species, is the first member of the genus known to occur in subsaharan Africa. It can be recognized by its all black gaster and proportions of the flagellomeres. The type series was collected 27 km SSE of Naivasha in the Rift Valley Province of Kenya. *Didineis nigricans* Morice, 1911, from Algeria is redescribed.

Didineis is a genus of 26 currently known species (Bohart and Menke 1976, Guichard 1990). Of them, 17 are Palearctic (ranging from Great Britain to Japan, and from Denmark to Algeria, Turkey, and Turkmenistan), 7 are Nearctic (Pennsylvania to Florida, Washington to Baja California, extending south to Nuevo Leon State in Mexico), 1 is Neotropical (Cuba only), and 1 Oriental (Bengal). During a recent expedition to Kenya, Jere S. Schweikert and I collected a series of specimens of a previously unknown species, the first to be found in subsaharan Africa. *Didineis nigricans* Morice, a little known species from Algeria, is redescribed as a byproduct of this study.

The family group names used in the title are based on Menke (1997) and Melo (1999). The morphological terminology follows Bohart and Menke (1976).

***Didineis massaica* Pulawski, new species**

Derivation of name.—*Massaica* is a Neolatin feminine adjective derived from the Massai people of Kenya in whose tribal area this species was collected.

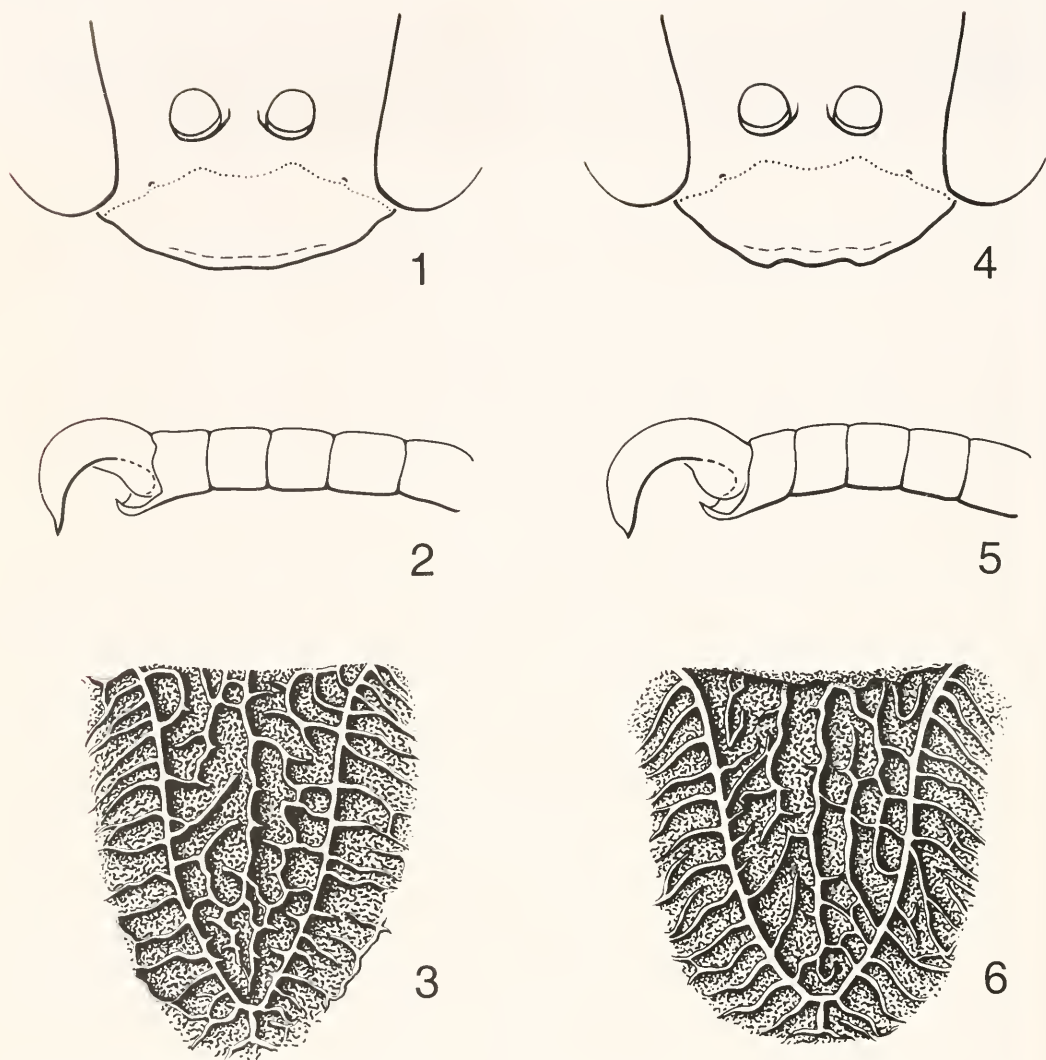
Diagnosis.—*Didineis massaica* differs from most of its congeners in having an all black gaster (rather than red at least

basally). The only other *Didineis* with an all black gaster are: *barbieri* (de Beaumont), *bucharica* Gussakovskij, the male of *latro* (de Beaumont), *nigricans* Morice (terga somewhat reddish apically), *orientalis* Cameron, *sibirica* Gussakovskij, and *turanica* Gussakovskij. Of these species, I have seen only the holotype of *nigricans* and one male of *latro*, but they can be distinguished from *massaica* by the characters detailed below following the original descriptions of Cameron (1897), de Beaumont (1967, 1968), and Gussakovskij (1937), Tsuneki's (1968) description of *Didineis sibirica nipponica*, and the key by Nemkov (1995):

Didineis barbieri from Algeria (female unknown) has flagellomere I and IX about $1.3 \times$ and less than $1.0 \times$ as long as wide, respectively. In *massaica*, these ratios are about 2.0 and 1.0 respectively.

Didineis bucharica from Uzbekistan (female unknown) has flagellomeres I–III somewhat expanded laterally, and flagellomeres III and IV no longer than wide. In the male of *massaica*, the respective flagellomeres are cylindrical and longer than wide.

Didineis latro from Turkey has a black scape, appressed tergal setae, and no tergal fasciae. In *massaica*, the scapal venter is yellow, tergum I bears several erect setae laterally, and at least tergum I has a broadly interrupted setal fascia.



Figs. 1-6. *Didineis* species: 1-3, *Didineis massaica*: 1, male clypeus. 2, apical male flagellomeres. 3, propodeal enclosure. 4-6, *Didineis nigricans*: 4, male clypeus. 5, apical male flagellomeres. 6, propodeal enclosure.

Didineis nigricans from Algeria (female unknown) has an obtusely tridentate clypeal free margin (Fig. 4) and flagellomere I about as long as wide. In the male of *massaica*, the clypeal free margin is evenly arcuate and flagellomere I is about $2.0 \times$ as long as wide.

Didineis orientalis from Bengal (female unknown) has yellow markings on the tegula and tibiae, whereas such markings lack in *massaica*.

Didineis sibirica from Eastern Siberia and Japan

has female flagellomeres about $2.0 \times$ as long as wide, and male flagellomeres I and IX about $1.5 \times$ as long as wide, respectively. In *massaica*, female flagellomeres II and IX are about $2.5 \times$ and $1.5 \times$ as long as wide, respectively, and male flagellomeres I and IX are about 2.0 and $1.0 \times$ as long as wide, respectively.

Didineis turanica (female unknown) has the median and penultimate flagellomeres longer than wide, forefemur with ventral margin

somewhat flattened, and foretibia slightly broader apically than near the midlength. In the male of *massaica*, flagellomeres VIII and IX are about as long as wide, the forefemur is not flattened (ventral margin evenly arcuate), and the foretibia is not broadened apically.

Description.—Frons finely, evenly punctate, punctures less than 1 diameter apart (averaging more than 1 diameter apart on interocular area and between ocelli and orbits). Pronotum with no transverse carina. Mesoscutum evenly punctate, punctures about 1 diameter apart. Mesopleuron dull, punctate (punctures less than 1 diameter apart except more posterovertrally), without well-defined ridges posterovertrally. Propodeal enclosure narrow, acutely angulate apically (Fig. 3); side irregularly ridged, apicolateral spine well defined, as in *lunicornis* Fabricius (the type species of the genus). Tergal punctures well defined.

Mesopleural setae in female denser below scrobal sulcus than on remaining surface, almost forming a discrete patch. Tergum I with apical, broadly interrupted setal fascia (also II and III in one of the males examined). Tergum I laterally with erect setae (some setae on remaining terga also erect).

Head, thorax, and gaster black (including flagellum and pronotal lobe), but mandible yellowish red mesally, scapal venter pale yellow, and tegula dark brown in one of the males. Femora black in female except forefemur reddish brown ventrally and apically; in male forefemur reddish brown except dorsum black in basal half, midfemur reddish brown except dorsum black, and hindfemur all black or with brownish outer surface. Tibiae reddish brown, mid- and hindtibiae darkened apically. Tarsi dark brown. Wing membrane slightly infumate, with darker fascia that covers all marginal cell, distal portion of submarginal I, all of submarginal II, distal part of discoidal II, an area of varying

width distad of discoidal II, and in female submarginal III.

♀—Clypeus uniformly, closely punctate except impunctate and shiny anteromesally (impunctate area about as long mesally as basal punctate area); free margin tridentate. Length of flagellomere II about $2.5 \times$ width, of flagellomere IX about $1.5 \times$ width. Dorsoexternal hindtibial setae suberect, shorter setae interspersed with longer ones.

♂—Clypeus uniformly, closely punctate, free margin nearly straight mesally (Fig. 1). Scape not concave laterally. Flagellomeres I–X cylindrical (flagellomere X with usual apicoventral expansion); dorsal length of I about $2.0 \times$ apical width, equal to that of II whose length is about $1.7 \times$ width, following articles progressively shorter, VIII and IX about as long as wide; flagellomere XI markedly curved, with sharp apex (Fig. 2). Foretibia and foretarsus not widened.

Records.—Holotype: ♂, Kenya: Rift Valley Province, 27 km SSE Naivasha at $0^{\circ}54.6'S$ $36^{\circ}31.0'E$, 3 June 1999, W.J. Pulawski and J.S. Schweikert (California Academy of Sciences). Paratypes: same data and depository (1 ♀, 2 ♂).

Didineis nigricans Morice (Figs. 4–6)

Didineis nigricans Morice, 1911:111, ♂. Holotype: ♂, Algeria: Biskra (Oxford University Museum).—Gussakovskij, 1937: 616 (original description copied, discussion of characters); R. Bohart and Menke, 1976:459 (listed).

This distinctive species is known from a single specimen collected more than 100 years ago that has never been reexamined since the original description. The latter omits some important structures (e.g., the shape of the propodeal enclosure) and inaccurately depicts some structures (e.g., "clypeus evidenter tridentatus").

Diagnosis.—The male of *nigricans* can be immediately recognized by its obtusely tridentate clypeal free margin (Fig. 4) and by the proportions of the flagellomeres

(flagellomere I about as long as wide, II about $1.5 \times$ as long as wide, VIII and IX as long as wide).

Description.—Frons finely, evenly punctate, punctures about 1 diameter apart (several diameter apart on interocellar area and between ocelli and orbits). Pronotum without transverse carina. Mesoscutum evenly punctate, punctures averaging about 2 diameters apart. Mesopleuron dull, somewhat irregularly punctate, with punctures no more than 1 diameter apart except episcrobal area shiny, with punctures more than 1 diameter apart, without well-defined ridges posteroven-trally. Propodeal enclosure somewhat broadened and not acutely angulate at apex (Fig. 6); side irregularly ridged, apicolateral spine slightly shorter than in *lun-icornis*. Tergal punctures well defined, but markedly smaller on tergum I than on remaining terga.

Gastral terga without setal fasciae. Tergum I laterally with erect setae.

Head, thorax, and gaster black (including flagellum and pronotal lobe), but mandible reddish mesally and scapal venter reddish brown, and apical depressions of terga reddish from certain angles. Femora reddish brown (hindfemur somewhat darkened basally), tibiae and tarsi reddish. Wings membrane slightly infumate, with marginal cell, submarginal cell II, and dorsoapical portion of discoidal cell II minimally darker.

♂.—Clypeus uniformly, closely punctate, free margin obtusely tridentate mesally (Fig. 4). Scape not concave laterally. Flagellomeres I-X cylindrical (flagellomere X with usual apicoventral expansion); dorsal length of I about equal to apical width and equal to 0.75 of II (whose dorsal length is $1.5 \times$ apical width); III-VII becoming gradually shorter, VIII and IX as long as wide; flagellomere XI markedly curved, with apex sharp (Fig. 5). Foretibia and foretarsus not widened.

Collecting date.—29 May 1898.

Material examined.—Only the holotype was seen.

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A Revision of *Entomosericus* Dahlbom 1845 (Hymenoptera: Apoidea: "Sphecidae") with Description of a New Species

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Abstract.—*Entomosericus* Dahlbom, 1845, is a palearctic genus with three species: *E. hauseri* Schmid-Egger, new species, from Israel, Jordan and southern Turkey, *E. kaufmani* Radoszkowski from southern-central Asia, and *E. concinnus* Dahlbom from eastern and southern Mediterranean area, Ukraine and Russia. *E. concinnus rufescens* de Beaumont is synonymized with *E. concinnus* (new synonym). A key to species identification is presented. A lectotype of *E. kaufmani* is designated. Gastral color is determined unsuitable for distinguishing species.

Entomosericus Dahlbom, 1845, is a palearctic genus of three species. Bohart and Menke (1976) and Menke (1997) placed it in its own subfamily because they could not associate it with any other sphecid group. Kazenas and Alexander (1993) suggested a relationship to the clade of Nysosinae (now Bembecinae sensu Menke 1997), Philanthinae and Astatinae based on larval characters. Melo (1999) finally proposed a relationship to the Pemphredoninae. He considered *Entomosericus* as a sister subtribe to the Psenini (sensu Bohart and Menke 1976).

Two species of *Entomosericus* have been described: *E. concinnus* Dahlbom, 1845, from the Greek island Rhodos and *E. kaufmani* Radoszkowski, 1877, from central Asia. In current keys, the two species have been primarily distinguished through color.

According to Balthasar (1972), all of the terga are black in *E. concinnus* while the first two or three terga are red in *E. kaufmani*. Pulawski (1978) also described the respective form of antennal flagellomere XI as a distinguishing character.

De Beaumont (1965) noted a broad geographic variation in color and punctuation in these species. He noted that all males of *E. concinnus* from Rhodos, Corfu, mainland Greece, and Croatia have black terga (also

Handlirsch 1888), while females from the mainland Greece have red terga I and II. Later, he (1967) reported two females of the species from Turkey with red basal terga, considering the presence of *E. kaufmani* in the western Palaearctic to be doubtful.

My own studies confirmed the observations of de Beaumont (1965, 1967). Additionally, a new species from the eastern Mediterranean area was found. Sternal and antennal characters allow males to be reliably distinguished and the geographical distribution of the species to be delineated. Females of the species remain difficult to distinguish and require comparison with determined material to be identified.

Sources of material.—Specimens from the following institutions were examined (abbreviations used are given):

Arens	coll. Werner Arens, Bad Hersfeld, Germany
CAS	California Academy of Sciences, San Francisco, California, USA
Hartmann	coll. Peter Hartmann, Bayreuth, Germany
Hauser	coll. Martin Hauser, Univ. Illinois, Urbana, USA
MCZL	Musée Cantonal der Zoologie, Lausanne, Switzerland

NHMW	Naturhistorisches Museum, Wien, Austria	ZMHB	Zoologisches Museum der Humbold-Universität, Ber- lin, Germany
Niehuis	coll. Oliver Niehuis, Mar- burg, Germany	ZMUM	Zoological Museum of the Moscow State University
OLL	Oberoesterreichisches Lan- desmuseum, Linz, Austria	ZSM	Zoologische Staatssammlung, Muenchen, Germany
SE	coll. Christian Schmid-Eg- ger, Berlin, Germany	<i>Technical terms.</i> —The morphological ter- minology employed in this paper follows Bohart and Menke (1976).	
SMNS	Staatliches Museum für Na- turkunde, Stuttgart, Germany		

KEY TO SPECIES OF *ENTOMOSERICUS*

Males

- 1. Flagellomere XI shovel-like, flattened (ventral surface is concave), narrower than more based flagellomeres, curved downwards (Fig. 3). Middle flagellomeres with ill-defined lateral tyloids (Fig. 3). Sternum VIII nearly flat, without lateral thickening, with long setae (Fig. 7). Inner (transparent) appendix of gonostylus twice as wide as outer (opaque) appendix, the latter with long setae (Fig. 6). Disk of sternum II with evanescent punctures that are 4–6 diameters apart, sternal surface shiny, unsculptured. Central Asia *kaufmani* Radoszkowski
- Flagellomere XI excavated beneath, nearly as wide as more basal flagellomeres. Flagellomeres with well-defined central tyloids (Fig. 1, 2). Sternum VIII uneven, with lateral thickening, asetose or with short setae (Fig. 10, 11). Inner (transparent) appendix of gonostylus half as wide as outer (opaque) appendix (Fig. 4), the latter asetose. Disk of sternum II with more densely arranged punctures that are 0.5–3 diameters apart. Eastern and southwest Mediterranean area 2
- 2. Flagellomeres VIII–XI reddish. Lateral thickening of sternum VIII with an oval concavity (Fig. 11). Sternum II unsculptured between punctures, with short setae. Tyloids on flagellomeres VII–VIII well-defined, flagellomere VI with pointed tyloid, flagellomere IX with ill-defined lateral tyloid (Fig. 1). At least tergum I red (southern Turkey to Israel, northwest Africa) or terga black (Europe to Turkey). France?, eastern Mediterranean area, southwest central Asia, northwest Africa *concinus* Dahlbom
- Flagellomeres black. Lateral thickening of sternum VIII evenly convex (Fig. 10). Sternum II microsculptured between punctures, nearly asetose. Tyloids on flagellomeres VII–VIII smaller, flagellomeres VI and IX both with a minute, ill-defined tyloid (Fig. 2). Terga black. Southern Turkey, Israel, Jordan *hauseri* Schmid-Egger, new species

Females

- 1. Shiny area between lateral ocellus and eye extending to eye margin (Fig. 12). Clypeal free margin with five distinct teeth, median teeth prominent, distinctly larger than lateral teeth (Fig. 15). Sternum II with fine and scattered, similiary sized punctures, that are many diameters apart. Terga I and II red. Central Asia *kaufmani* Radoszkowski
- Shiny area between lateral ocellus and eye smaller, and not extended to eye margin, or absent (Fig. 13, 14). Medial teeth of the clypeal free margin less prominent, not distinctly larger than lateral teeth (figs 16, 17). Sternum II with uneven sized punctures that are unevenly distributed and about 1–3 diameters apart. Terga I and II red or black. Eastern and southwest Mediterranean area 2
- 2. Shiny area between lateral ocellus and eye essentially absent (Fig. 14). Gaster black. Punctuation of sternum II denser than in *concinus*, punctures 0.5–1.5 diameters apart. Surface

- of sterna more densely microsculptured, not shiny. Tergum II without a distinct step, or edge, at the base of the apical tergal depression. Apical tergal depression of tergum II markedly broader medially. Southern Turkey, Israel, Jordan *hauseri* Schmid-Egger, new species
- Shiny area between lateral ocellus and eye larger, about as large as lateral ocellus (Fig. 13). Gaster red basally (at least tergum I red in specimens from southern Turkey, Israel, Jordan) except all black in specimens from Rhodos Island (Greece) and western Turkey. Punctures of sternum II less dense arranged, separated by 1–3 diameters, interspaces shiny. Tergum II usually with a distinct step, or edge, at the base of apical tergal depression. France?, eastern Mediterranean area, southwest central Asia, northwest Africa . . . *concinus* Dahlbom

Entomosericus Dahlbom

Entomosericus Dahlbom 1845: 486. Type species *Entomericus* (sic) *concinus* Dahlbom 1845, by monotypy. Spelled *Entomosericus* by Dahlbom, 1845, on Tabula Examinationis Synoptica Generum Nyssonidarum.

Entomosericus hauseri Schmid-Egger, new species

(Figs. 2, 4, 5, 9, 10, 14, 16, 18)

Diagnosis and discussion.—The male of *Entomosericus hauseri* is easily distinguished from *concinus* by its different form of sternum VII. Also, the tyloids and setae of last sternum differ from those of *concinus*. The female closely resembles *concinus*, but punctures are denser than in that species. Also, both sexes are different in color from *concinus* in the areas where they occur sympatrically. *E. hauseri* is black, while *concinus* has red terga. Only in Turkey might black males of both species occur together.

Male.—9–11 mm. Body black, tarsal segments and lateral parts of tergum I reddish. Head densely punctate, including area on each side of lateral ocellus (cf. Fig. 14). Clypeal free margin with five small teeth, outer tooth minute, nearly rounded. Inner margin of eye and clypeus with long setal fascia. Face with long erect setae. An-

tenna black, with small, oblong tyloids on venter of flagellomeres VII–VIII and point-form tyloids on flagellomere VI and IX (Fig. 2). Tyloids smaller and less distinct than in *concinus*. Thorax and upper part of head with long silver setae. Thorax including scutellum and propodeum densely punctate, interspaces shiny. Lower mesopleuron inpunctate, shiny. Gaster and legs only with short setae. Terga I and II without microsculpture, punctures 0.1–1 diameters apart. Terga III–VII rugulose. Sterna microscopically punctate, interspaces microsculptured, sterna II and III with dense, coarse punctation, punctures 0.1–1 diameters apart. Disk of sternum II of smaller specimens nearly unsculptured. Sternum VIII: Fig. 10. Setal fascia at distal margin of sterna III and IV small, setae very thin and short (half as long as in *concinus*). Sterna VI and VIII (in profile) with very short, erect setae (Fig. 9). Genitalia: Figs. 4, 5. Inner translucent appendix of gonostylus half as wide as outer (opaque) appendage. Wing venation and stigma dark brown, costal venation yellowish, wing membrane slightly darkened, yellowish-brown.

Female.—9–10 mm. Body black, with apex of tergites, sides of tergum I and tarsal segments slightly reddish. Punctures denser and larger than in *concinus*. Head

→



1a



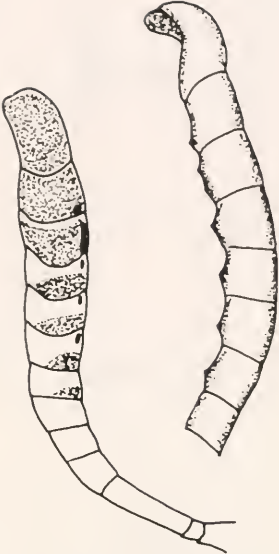
1b



2a



2b



3a



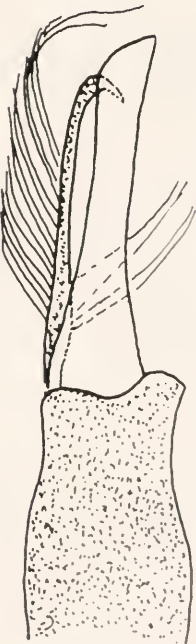
3b



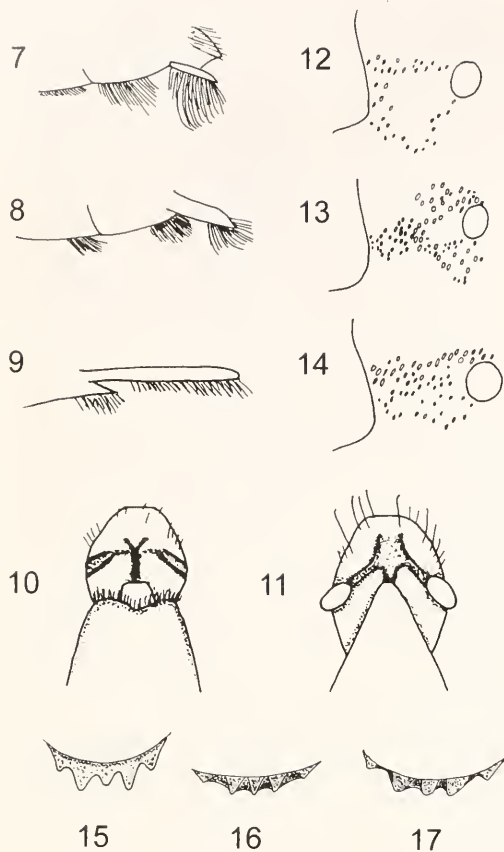
4



5



6



Figs. 7-17. *Entomoceriscus* spp. 7-9, male sterna VI-VIII, lateral view. 7, *E. kaufnani*. 8, *E. concinnus*. 9, *E. hauseri*. 10-11, sterna VII-VIII, ventral view. 10, *E. hauseri*. 11, *E. concinnus*. 12-14, punctation of female between eye (left) and lateral ocellus. 12, *E. kaufnani*. 13, *E. concinnus*. 14, *E. hauseri*. 15-17, clypeal free margin of female. 15, *E. kaufnani*. 16, *E. hauseri*. 17, *E. concinnus*.

densely punctate, including area on each side of lateral ocellus (Fig. 14). Clypeus basally minutely, densely punctate, apically with longitudinal ridges (Fig. 16). Scutellum smooth and shiny basally, coarsely, longitudinally ridged apically. Punctures of tergum I 1-2 diameters apart, without punctures on disk. Punctures of terga II-V 2-3 diameters apart, punctures half as wide as in *concinnus*. Tergum II without a distinct step, or edge, at the base of the apical tergal depression. Apical tergal depression of tergum II markedly

broader medially. Punctures of sternum II 2-3 diameters apart. Sterna II-VI finely and densely microsculptured, basolateral corner finely, densely punctate. Wings venation dark brown, wing membrane slightly darkened.

Habitat.—In northern Israel, *hauseri* was found in the Mediterranean climate area with limestone substrate. The specimens were flying near the ground in grass on small paths and were collected by sweeping plants. There were unused fields and cattle pasture nearby.

Etymology.—The species is dedicated to Martin Hauser, a friend and specialist of Stratiomyidae (Diptera), who supported the expedition to Israel in 1996.

Geographic distribution (Fig. 18).—Israel and Jordan to southern Turkey.

Type material.—HOLOTYPE male: ISRAEL, 40 km NE Haifa, 1 km E Hurfeish, 33.01°N 35.21° E, 16.05.1996 leg. SE (ZSM). PARATYPES: ISRAEL: 40 km NE Haifa, 1 km E Hurfeish, 33.01°N 35.21° E, 16 May 1996 8 males (SE, Hauser); 15 km E Qiryat Shemona, Foothill of Hermon, 33.15° N 35.44° E, 17 May 1996 2 males (SE). JORDAN: Jarash 1 May 1996 1 male (OLL); North Shuna 30 April 1996 1 female (OLL). TURKEY: Mardin, 23 May 1988 2 males (SE); Urfa, 3 June 1988 1 female (MCZL); 25 km E Golbasi 7 June 1998 6 males 11 females (OLL); 10 km NW Gaziantep 20 June 1997 1 male (OLL); N. of Akseki, 19 June 1998 7 males (OLL); Tuzlagozu (Baykan) 4 June 1998 1 male (OLL); Kahraman Maras, 40 km SE, 10 June 1998 19 males 1 female (OLL); 30 km N Erdemli, Aslani 17 June 1998 1 male 1 female (OLL)—Gaziantep, Nizip 27 May 1978 1 male (CAS); Kuzuzcebelen/Mersin 25 May 1998 1 male (OLL).

***Entomoseriscus concinnus* Dahlbom 1845**
(Figs. 1, 8, 11, 13, 17, 19)

Entomoseriscus concinnus Dahlbom, 1845: 486, male, Holotype or syntypes: Greece, Rhodos Island (Lund)

Entomoseriscus concinnus rufescens Beau-



Fig. 18. Collecting localities of *Entomosericus hauseri* in the eastern Mediterranean.

mont 1950: 403. Holotype: female Algeria, Taouiala (MCZL). **New Synonym.**

Diagnosis and discussion.—The male of this species is easily characterized by the form of sternum VIII and the flagellomeres. Females may be distinguished from the other species by punctuation and other characters (see key). *Entomosericus concinnus* has been confused with *kaufmani*. However, *concinnus* occurs only in the western Palearctic, whereas *kaufmani* is a central asian species. The ranges of the species overlap in the Ural river area in northern Kazakhstan and Russia. *E. concinnus* has two color forms. In Europe and northern and central Turkey the male gas-

ter is all black, while in southern Turkey, Syria, Israel and northwest Africa the gaster base is red. Females of the species have a red gaster base except in specimens from Rhodos (the type locality) and western Turkey, where the gaster is all black. The isolated color form in the Dahlbom's type material might have caused confusion for earlier authors (Handlirsch 1888). Females with an all black gaster have not been found in other areas. The subspecies *concinnus rufescens* Beaumont, which was described from northwest Africa, is only a light color form of the species. It differs slightly from typical *concinnus* (see below), which itself is variable in the extend of gaster coloration in the eastern Mediter-

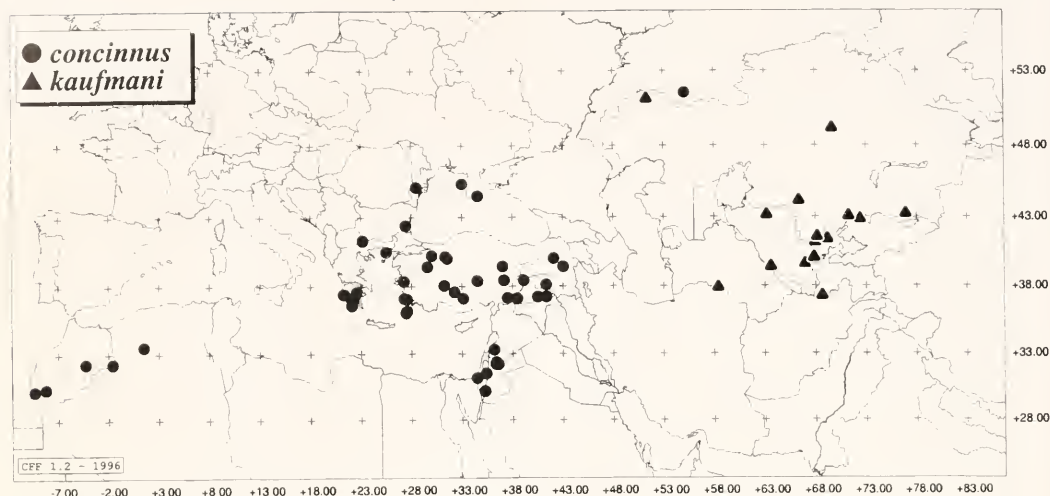


Fig. 19. Collecting localities of *Entomosericus concinnus* and *E. kaufmani* in southern Europe, western and central Asia and northern Africa.

ranean area. Males of *concinnus concinnus* from Syria and Israel are similar to males of *concinnus rufescens* from north-west Africa, while females of *concinnus rufescens* have a more light red gaster than females of *concinnus concinnus*. Therefore, the status of *rufescens* as a subspecies of *concinnus* is not justified due to the observed variability in *concinnus*.

Male.—9–12 mm. Body black, or with red basal terga. Tarsi red. Head densely punctate, shiny area between eye and lateral ocellus present (cf. Fig. 13). Clypeal free margin with five small teeth. Upper part of face with long erect setae. Dorsal side of flagellomeres VIII–XI, surface of flagellomere X–XI red. Flagellomeres VII–VIII with large and well-defined tyloids; flagellomere VI with small, pointed tyloid; tyloid at flagellomere IX indistinct, ventrolaterally situated (Fig. 1). Body sparsely punctate. Thorax with long, silver setae. Thorax surface and mesopleuron with shiny interspaces, punctures 1–2 diameters apart. Terga I–II coarsely punctate, punctures 0.2–1 diameter apart. Terga III–VI finely, densely punctate. Disk of sternum II shiny, coarsely and densely punctate, punctures 1–3 diameters apart. Sternum II laterally in specimens from Tur-

key, Europe with fine, dense punctation; in specimens from southern Turkey, Israel, Morokko with the same punctation as disk. Sterna III–VI more or less microsculptured, finely, densely punctate. Lateral thickening of sternum VII with an oval concavity (Fig. 11). Lateral edge of sternum III with long band of brown setae. Sternum VIII (in profile) with dense erect setae as long as fourth tarsal segment of hind leg, sterna V and VI with erect setae (Fig. 8). Genitalia similar to that of *hausseri* spec. n. Wings venation and stigma dark brown, costal and basal venation yellowish, wing membrane slightly darkened yellowish brown.

Female.—10–11 mm. Body black, or with red basal terga. Tarsi partly red. Head densely punctate, area beside lateral ocellus smooth and shiny (Fig. 13). Clypeal free margin with five rounded teeth (Fig. 17), often worn down. Clypeus apically longitudinally ridged. Mesoscutum with smooth spaces between longitudinal punctures. Punctuation of thorax variable, but punctures of mesoscutum at least many diameters apart. Anterior part of scutellum smooth, posterior part longitudinally wrinkled. Mesopleuron densely punctate in upper part, punctures in lower part

many diameters apart. Terga I-III distinctly and densely punctate, punctures 0.2–1 diameter apart. Base of terga III-IV with denser punctation than the apex. Apical margin of tergum II variable: in specimens from Europe and Turkey it is straight (or barely emarginated) and strongly stepped with keel basally (a step between disk of tergum II and apical tergal depression); in specimens from Israel and Jordan it is slightly rounded; in specimens from Morocco and Algeria it is barely stepped, with a rounded basal edge. Sternum II with a few deep punctures of variable diameter (1–2 diameters apart), with fine microsculptured between punctures. Wing venation dark brown except with yellowish basal venation in specimen not from southern Turkey.

Variation.—Males and females from Morocco differ slightly from Turkish and Greek specimens: Diameter of punctures of the terga and sterna are half as wide. The apical margin of tergum II is barely dented with a rounded flat basal edge.

Color variation.—Europe, northern and central Turkey, Russia and Ukraine: Males with all terga black; females with tergum I and II red. Rhodos island (Greece) and Western Turkey (Aegean coast): Males and females with all terga black. Syria, Israel, southern Turkey and Jordan: Males with tergum I red and tergum II black with red parts; females with terga I-II red. Northwest Africa: Males with tergum I and base of tergum II red. Females with terga I-III and base of tergum IV red, some specimens with tergum IV black.

Doubtful specimen.—A single female from Jordan (20km S North Shuna, Tall al Arbatin 19 April 1998, coll. SE) could not assigned to species. It has a black gaster (normally gaster base is red in Jordan), a shiny area with only few punctures between the lateral ocellus and the eye, the tergum II is as in average *concinus*. A male of *concinus* was collected on the same day at the same locality.

Geographic distribution (Fig. 19).—East-

ern mediterranean area to southern Russia and northwest Africa.

Records.—ALGERIA: Taouiala [33°54'N 01°51'E], Holotype of *E. concinnus rufescens* (de Beaumont 1950, in British Museum London). Not seen, but other specimens of type series examined. ARMENIA: Urcadzor 14 June 1988 1 male (gaster black) (OLL). BULGARIA: Melnik 23 May 1985 3 males 22 June 1997 2 males (OLL); Slancev Brjag 15 June 1997 1 male (OLL); Sandanski 14 July 1979 2 females (CAS); Slancev Brjag July 1972 1 female 2 males (OLL) (males: gaster black, females: terga I and II red); Albena 17 July 1978 1 female (OLL); Ivanski near Schumen 15–30 July 1969 1 male (coll Burger)? FRANCE: Gallia mer., Ancy, 1897 1 male (NHMW, gaster black). Specimen probably mislabeled. GREECE, MAINLAND: Alexandropoulos 16 June 1994 1 female (NHMW); Alt Korinth 28 May 1996 1 male; 7 June 1997 2 males 1 female (Arens); Korinth 15 May 1970 (ZMHB); Attika 1 male (NHMW); Cephalonia 4 males 1 female (NHMW) (det Maidl as *kaufmani*); Graecia, Argostoli? 26 May 1908 1 male 1 female (NHMW) (female det Maidl als *kaufmani*); Attika 1 female (NHMW) (det Maidl als *kaufmani*); Olympia 10 June 1961 1 female (CAS); Olympia, Alfios-Tal 4 June 1995 1 male (Arens); Kalamata, Avia 14 May 1995 2 females; 10 June 1996 2 females (Arens); Peloponnes, Midea 19 June 1996 1 female (Arens); Peloponnes, Sparta, Amyklai 5 June 1996 1 female 1 male (Arens); Peloponnes, Sparta, Menelaion 26 May 1997 3 males; 21 May 1997 2 males 1 female; 4 June 1996 6 males 6 females (Arens); Peloponnes, Sykion 8 June 1997 2 females (Arens); Olympia 19 June 1961 1 female; 1 June 1963 1 female 1 male (MCZL); Pyrgos 11 June 1961 3 females (MCZL); Kalamata 15 May 1964 2 females 5 males (MCZL); Nea Kefissia 19 June 1957 1 female 2 males (MCZL) (males: gaster black, females: terga I and II red); GREECE, RHODOS ISLAND: Kritinia, 2 May 1990 9 males 1 female (SMNS); Salakos, Kamiros 3 May 1990 2 males 2 females (SMNS); Rhodos, no specific locality, June 1939 3 males (MCZL); Rhodus, no specific locality, 1869 4 males 2 females (NHMW); W Apolakkia, N Monolithos 23 April 1998 1 male 1 female (Hartmann) (gaster black). HUNGARY: male, without date and exact locality, may be today's Romania (ZMHB, also referred by Handlirsch 1895: 850 gaster black); 'Ungarn coll. Hindlmayer' 1 male (ZSM). ISRAEL: Lehavim junction, 11 km N Be'er Sheva, 27 March 1991, 2 males (SE) (gastral base red). JORDAN: Petra 14 May 1995 3 males (OLL) (gastral base red); North Shuna 29 April 1996 1 female (OLL); 20km S North Shuna, Tall al Arbatin 19 April 1998 1 male (OLL) (gastral base black). MOROKKO: Agadir, 15 April 1947 1 male 1 female (MCZL, Paratype of *E. c. rufescens* de Beaumont); Itilit, 15 June 1962 1 male (MCZL, Paratype of *E. c. rufescens* de Beaumont); 50 km NE Taroudannt, 5 km E Kreuzung Tizn-Test/Aoulouz 12 April 1996 4 females (Niehuis, SE); 10 km

N Rich, 23 May 1995 1 female (OLL); 10 km S Bouarfa 20 May 1995 1 female (OLL); 40 km S Guercif 15 May 1995 1 female (OLL). ROMANIA: Dobrogea, Camaraua Fetii 26 June 1993 3 males (OLL) (gaster black); Tultscha [= Tulcea] 1859 1 female (leg. Mann, NHMW, terga I and II red); Mehadia [leg] Mann 1859 2 females (NHMW, gastral base red). Scobiola-Palade (1966) mentions *E. concinnus* and *E. kaufmani* from Romania, but the latter is probably the red form of *E. concinnus*. RUSSIA: Southern Ural, Kargala b. Orenburg, 1915–1917 1 male (ZMHB, gaster black). SYRIA: Mezzé near Damascus 21 May 1954 2 males 3 females (CAS, MCZL); Damascus, road to Kissoué 2–18 May 1960 2 males 1 female (MCZL); Marbi, 9 May 1996 1 male (OLL); 30 km s Suwayda, Dibbin 15–17 May 1996 1 male; 10 km SE Suwayda, Kafr 19 May 1996 1 male (OLL); Anata, 50 km SE of Suwayda 20–21 May 1996 1 female (OLL) (gastral base red). TURKEY: **First terga of males black, tergum I and II of females red:** Horasan, 18 km E Delibaba 25 June 1993 2 males (OLL); 30 km N Kutahya, Porsuk Baraji 15 June 1997 2 males (OLL); Gürün 7 June 1970 1 female (CAS); Konya, Karaman 11 June 1979 1 male (CAS); Urfa 21 May 1972 1 female (CAS); Sille, Konya, 16 June 1968 1 male (MCZL); Amasya 1,400 ft, 9 June 1959 1 male (MCZL); Asia minor 11 July 1852 1 female (ZSM); Osmaneli 14 June 1997 3 males 1 female (OLL); 40 km E Mut, Cornelek 29 May 1996 4 males 1 female (OLL); Capadocia, Ürgüp 13 June 1998 8 males 1 female (OLL); Capadocia, 10 km NW Ürgüp 15 June 1998 1 male 1 female (OLL); Tuzlagözü (Baykan) 4 June 1998 1 male (OLL); Bozkir 26 May 1998 1 male (OLL); Agri 27 June 1993 1 male (OLL); Göreme 23 June 1993 1 male (OLL); Konya, 30 km S of Aksehir 24 June 1998 1 male (OLL); 20 km SE Horasan, Delibaba 3 July 1997 1 female (OLL); Bolu, 17 km S Seben 17 June 1998 1 female (OLL); Manisa, 30 km E 20 June 1998 1 female (OLL); Hop Gecidi, Mardin 6 June 1998 1 female (OLL); Ankara, 40 km W Ayas 26 June 1998 1 female (OLL); Sivas, 45 km E Yarıhisar 24 June 1993 1 female (OLL); Taskesigi/10 km E Antalya 1998 18 males (OLL); Gevas/Van Gölü 29 June 1993 1 female (OLL); **Terga I and II of males red:** Elazığ 7 June 1980 1 male (SE); Urfa 20 May 1967 1 male (MCZL) -Halfeti (Birecik) 31 May 1998 1 male (OLL); Tuzlagözü (Baykan) 4 June 1998 1 male (OLL); Halfeti 3–5 May 1994 1 male (OLL). **Gaster of females black:** W-Turkey, SSO Milas, Camköy lake 20 June 1998 1 female (Niehuis); W-Turkey, SO Milas, Akyoi 19 June 1998 1 female (Niehuis). UKRAINE: Falzfeinowo a. Dnipro 12 May–7 June 1914 1 male (gaster black) (ZMHB); Otuzysches Tal, auf *Teucrium polium*, leg. Wuczetitz, 4 July 1926 1 female (NHMW, det. Maidl as *kaufmani*, tergum I and 2 red) (= probably Otuzy Valley or Otuzskaya Dolina in Crimea, Ukraine); Umg. Tokluk, near Sudak, at *Reseda lutea* 4 June 1924 1 male Wuczetitz [leg] (NHMW, gaster black) (= probably Sudak in Crimea, Ukraine)

Entomosericus kaufmani Radoszkowski
1877

(Figs. 3, 6, 7, 12, 15, 19)

Entomosericus kaufmani Radoszkowski 1877: 46. Male, female. Misspelled '*kaufmanni*' in most subsequent publications. Lectotype, male: Kasachstan, Kyzylkum [desert], 28 April 1871 (A.P.Fedchenko coll.) [appr. 43°13'N–71°35'E]. Designed as lectotype by A. Antropov (ZMUM).

Diagnosis.—The male of *Entomosericus kaufmani* is easily recognizable by its flat sternum VIII and its ventrally concave flagellomere XI. Females have a large shiny area between the lateral ocellus and eye. The species is smaller and more slender than *concinnus*. It occurs only in southern-central Asia from Kazakhstan to Turkmenistan (Kazenas and Alexander 1993). An isolated record comes from Uralsk in northern Kazakhstan. All examined '*kaufmani*' (det. Madl or Handlirsch, coll. NHMW) from Europe or Turkey are misidentifications of the red colored form of *concinnus*.

Male.—8–9 mm, Body black, tergum I and parts of tergum II red. Legs red except tibiae. Face covered with a dense silver pubescence in lower part and erect setae in upper part. Area between eye and lateral ocellus only with few punctures near eye (cf. Fig. 12). Clypeal free margin with 5 teeth, median tooth and lateral teeth distinctly smaller than mediolateral teeth. Flagellomere XI with a concave ventral surface which is ventrally curved. Ventral surface of flagellomeres V–IX with indistinct lateral tyloids and with half moon shaped red spots. Ventral surface of flagellomeres X–XI completely red, flagellomere XI also partly red on dorsal surface (Fig. 3). Punctuation of body less dense than in *concinnus*, spaces between punctures shiner than in *concinnus*. Punctures of terga I and II 0.5–2 diameters apart. Sterna II and III unsculptured with only few scattered punctures, that are separated by many diameters. Disk of sterna IV

and V finely and densely punctate, laterally only with a few coarse punctures. Sternum III with long band of setae (as in *concinus*), medial setae of band half as long as lateral setae. Sterna VI and VIII (sometimes V) with long silver setae (Fig. 7). Sternum VIII nearly flat, without lateral thickening. Inner transparent appendix of gonostylus twice as wide as outer opaque appendage (Fig. 6). Wings venation and stigma dark brown except yellowish costal and basal venation. Wing membrane slightly darkened.

Female.—9–10 mm. Body, including legs, black, terga and sterna I–II red. Head finely and densely punctate (punctures 0.5–1 diameter apart). Clypeus apically indistinctly longitudinal ridged, without punctation, basally finely punctate. Clypeal free margin with five well developed teeth. Shiny area between lateral ocellus and eye large, extending to eye, sometimes with scattered punctures (Fig. 12). Thorax unsculptured, shiny, coarsely punctate. Upper part of mesopleuron densely, finely punctate, lower part only with few punctures. Punctures at disk of terga I–II 1–2 diameters apart, punctures of succeeding terga more densely arranged. Edge between disk of tergum II and apical tergal depression rounded, apical margin of tergum II slightly dented. Disk of sterna II–III nearly unsculptured, sternum II with only a few scattered punctures that are many diameters apart. Wings venation dark brown, wing membrane slightly darkened.

Life history.—Kazenas and Alexander (1993) described the nest architecture and larva of *kaufmani* from southeastern Kazakhstan, Talas River. The females dig nearly vertical burrows in sandy soil and fill each cell with eight to 18 leafhoppers (Homoptera, Cicadellidae).

Type material.—PARALECTOTYPES (Lectotype see above): All designed as paralectotypes by A. Antropov. The type series is deposited in ZMUM and includes the following specimens: Zeravshan valley

9 May 1869 2 males (A.P. Fedchenko coll.) [appr. 39°33'N–63°40'E]; Zeravshan valley 23 May 1869 1 male (A.P. Fedchenko coll.); Chardara, 25 April 1871 2 males (A.P. Fedchenko coll.) [41°15'N–67°58'E]; Chardara 27 April 1871 1 female 1 male (A.P. Fedchenko coll.); Kyzylkum [desert] 28 April 1871 1 female (A.P. Fedchenko coll.) [appr. 42°40'N–63°37'E]; Kyzylkum [desert] 1 May 1871 2 males (A.P. Fedchenko coll.); Syutkent, 3 May 1871 1 male (A.P. Fedchenko coll.) [41°55'N–68°5'E]; Bayrakum [Baygakum] 4 May 1871 1 male (A.P. Fedchenko coll.) [44°18'N–66°28'E]; Karakskaya steppe 6 May 1871 1 female (A.P. Fedchenko coll.) [appr. 49°18'N–69°50'E].

Geographic distribution (Fig. 19).—Southern-central Asia from Kazakhstan to Turkmenistan.

Records.—KAZAKHSTAN: 2 females 1 male from coll Radoszkowski (ZMHB), [male without locality, females from Chardara and Kyzylkum (in russian letters), all labelled as 'Type', probably belonging to the syntypes serie, not designated as paralectotypes]; 10 km E Ddambul 31 May 1994 6 males 3 females (OLL) -Darbaza 40 km N Tachkent 30 May 1994 4 males 8 females (OLL); Vanovka, 80 km E Ddambul 1 male (OLL); Alma Ata 1 May 1994 1 female (OLL); 10 km N Chayan 1 male (CAS); vicinity of village Togusken on Talas River 1 female (CAS); vicinity of Uralsk 1 female (CAS). TADJIKISTAN: 3 km W Dusti, 130 km S Duchanbe 15–16 May 1991 1 female (OLL). TURKMENIA: Sandikazi 3–13 May 1993 18 males 3 females (OLL); Askahbad 22 May 1964 1 male (CAS); Star. Nisa/Ashabad 28 April 1977 1 male (OLL). UZBEKISTAN: Samarkand 19–21 May 1994 ca. 200 males ca. 40 females (OLL); Czirczik 28 May 1994 14 males 5 females (OLL); 5 km W Ddjizak 23 May 1994 9 males 6 females (OLL); Djuma 1 male 1 female (CAS)- Samarkand: Chupan-Ata-Mountain 2 males 2 females (CAS)- Sary-Agach in Tashkent Distrikt 1 male (CAS).

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New Odour Glands in *Xylocopa* Males (Hymenoptera: Apoidea: Anthophoridae)

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Abstract.—Odour glands were found in all tergites in males of the neotropical *Xylocopa bimaculata* Friese and *X. nigrocincta* Smith as well as in the palaearctic *X. violacea* Linné. Furthermore odour glands were found in the fore, middle and hind legs of *X. bimaculata* and *X. nigrocincta*. Males of *X. bimaculata* and *X. nigrocincta* establish non-resource based territories to which they attract females by spreading secretions of the odour glands over their body. For this they brush with specialized hairs on their hind legs over the abdomen, which they extend in order to expose the pores of the odour glands. The function of glands in all three pairs of legs is discussed in comparison with similar findings of odour glands in other species of carpenter bees and leafcutter bees.

Territorial male carpenter bees that actively search for females establish two kinds of territories: at nesting sites or at flowering plants (Hurd and Linsley 1975, Alcock 1991). Such territories may cover an area of several square meters. Other males attract females with sex pheromones to territories which contain neither nests nor food plants, so called non-resource based territories. These territories may cover a space less than one cubic meter, in many cases they measure 10 to 15 cm³. In some species a single male establishes its territory alone, for example in a tree. In others conspecific males establish their non-resource based territories together in close vicinity, forming so called leks. In these cases the distance between single territories may be as short as one meter.

Males in non-resource based territories have to cope with two problems: they have to leave their territories in order to find nectar as energy for their long lasting territorial flights. In *Xylocopa nigrocincta* males dehydrate the nectar that is fed to them by the mother in the nest. Thereby they get rid of excess water, and with a

higher concentration of sugar they improve their energy budget. Of males with the same amount of sugar in their crop those fly longer in their territories which have diluted the sugar in small volumes of water (Wittmann and Scholz 1989).

Furthermore their success in attracting a female depends on the amount of pheromones secreted per time. This may be one of the reasons why males establish their territories close to each other in leks. The advantage of such leks is probably that together the males have better chances to attract a female.

Within the genus *Xylocopa*, odour glands have been described from the head (mandibular gland) and from the thorax (mesosomal gland) (Wheeler *et al.* 1976, Vinson *et al.* 1986). Furthermore odour glands were found recently in the fore legs of some Old and New World *Xylocopa* males (Wittmann and Blochtein 1995).

Males of *X. hisutissima* and *X. sulcatipes* have been reported marking their mating territories with the secretions of the mandibular glands (Velthuis and Camargo 1975 a & b, Hefetz 1983). Territorial males can identify conspecific males as intruders of

their territory by the secretions of the mandibular glands. In consequence this odour elicits defence behaviour in the owner of the territory (Velthuis and Camargo 1975 a & b). Mesosomal glands are male specific. The males frequently brush their legs over their body thereby spreading the odour (Vinson *et al.* 1986). The secretions of these glands are supposed to act as territorial pheromones in non-resource based territories (Gerling *et al.* 1989).

MATERIAL AND METHODS

All observations on behaviour were made between September and November 1995 in the natural habitat in the forest reservation area Pró-Mata of the PUC-University Porto Alegre (Brazil). The area is located in the northern highlands of Rio Grande do Sul, the Serra Geral (50°–51° W and 29°–30° S) in an elevation of ca. 900 m, about 150 km north of Porto Alegre.

For identification we used the key to subgenera by Hurd and Moure (1963). Furthermore the bees were compared with the collection of the Biological Research Station of the University of Tübingen/Germany at the PUC-University in Porto Alegre, Brazil. Critical species were identified by Dr. J. S. Moure.

To analyse the territorial behaviour males were filmed during the territorial flight with a Panasonic F15.

For SEM-analysis we used a Stereoscan 250 Mk2 and a Hitachi S-800. The bees, or parts of them, were macerated in 5 % KOH for 24 hours, after which they were dehydrated in 50–100 % ethanol and dried for 24 hours at 30°C. If glands with chitinized ducts are present, these structures remain after the mazeration.

To check the presence of volatile substances in the area of glandular pores we washed the abdomen of a freshly killed territorial male in pentane. The samples were analyzed with a Fisons MD-800 GC-MS on a fused silica column, DB-5 (15 m × 0.32 mm), the temperature was programmed from 80°C (for 2 min) to 200°C at 10°C/min.

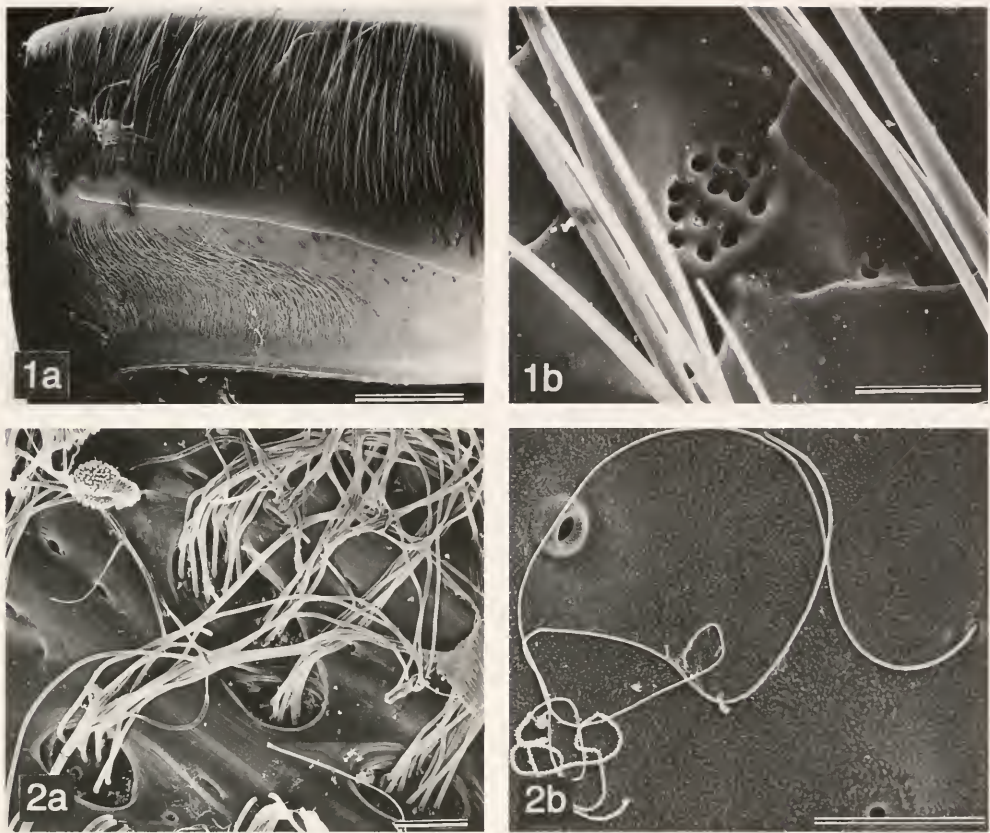
Compounds were identified by their mass spectra and using Kovats indices.

RESULTS

Abdominal glands.—SEM analyses of the sternites and tergites of *X. bimaculata* revealed that pores of odour glands are present in tergites I–VI. These pores are located on the frontal part of the tergites which are hidden under the anterior tergites (Fig. 1a). They are the openings of chitinous ducts which lead into glandular cells in the abdomen. After maceration these ducts are visible on the inner surface of the tergites. In tergites I–V we found the highest amount of pores. On tergite I and II the pores were scattered, while on tergites III, IV and V most of the pores appeared clumped. Between 10 and 20 pores were grouped in round areas with a diameter of 8–10 µm (Fig. 1b). The distances between these areas ranged between 20 and 40 µm. On the inner side of the tergite these groups of pores correspond with a bundle of cuticular ducts of odour glands (Fig. 2a). The terminal part of each duct is covered with short lateral ducts. This end apparatus is normally inside the glandular cell that has been macerated (Fig. 2b). In tergite VI only a few scattered pores were found, mostly on the lateral parts of the tergite.

Description of hairs on the abdomen.—Noteworthy are three different types of hairs on the tergites. On those parts of the tergites that are covered by the anterior tergites the hairs are plumose and about 200 µm long. The hairs on the posterior part of the tergite are unbranched and between 0.5 and 1 mm long. Most conspicuous are the bunches of bristles on the sides of the last three tergites.

Abdominal glands in males of other Xylocopa species.—We also found pores of odour glands in all tergites of *X. nigrocincta* and in *X. violacea*. In both species single pores have also a diameter of 2 µm. However, they are not arranged in groups as in *X. bimaculata*. The chitinous ducts of



Figs. 1–2. 1, Outer surface of *X. bimaculata* tergite IV: 1a, The median of the tergite is on the right borderline, the pores are hidden under the dense coverage of short hairs; 1b, Aggregation of 12 pores of odour glands. Each of the pores has a diameter of about 2 µm. 2, Inner side of the tergite IV: 2a, Bundles of cuticular ducts of odour glands, diameter of each duct is ca. 2 µm. 2b, Cuticular duct and the terminal apparatus. Scale bars: 1a) 1 mm, 1b) 10 µm, 2a) 20 µm, 2b) 40 µm.

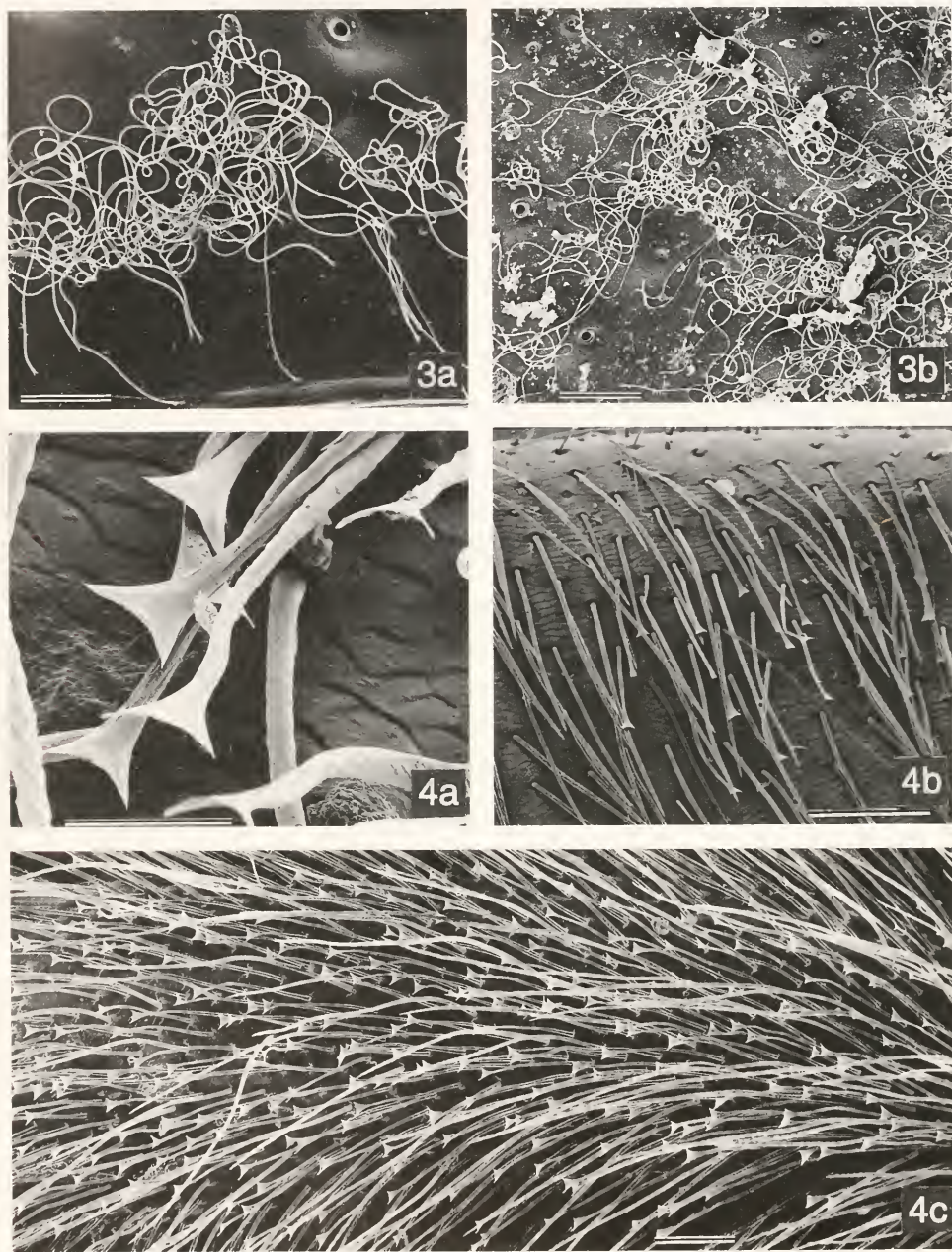
the odour glands have the same appearance in all three species (Fig.3a & b).

Glands in legs.—On the fore, middle and hind legs of *X. bimaculata* we found pores of odour glands. On the fore legs the pores were on the dorsal and anterior side of the basitarsus and also on the ventral side of the other tarsalia of the fore leg. On the middle leg pores were found on the dorsal side of the basitarsus, while on the hind leg the pores were found on the ventral side of the basitarsus. In *X. nigrocincta* pores were also found on the basitarsus of the fore leg.

Hairs on the fore legs.—A notable feature on the fore leg of *X. bimaculata* is a specific type of hair. When the male is viewed

frontally the hairs of the anterior side of the tarsalia and parts of the tibia appear shining white. The front leg bears on the anterior dorsal edge of the tarsalia a fan of bristles which are about three times as long as the diameter of the basitarsus. Such shiny white hairs are also present on the tarsi of the middle legs.

Hairs on the hind legs.—On the ventral side of femur and tibia of the hind legs we found a conspicuous type of hairs. They have smooth shafts and their tips are broadened and flattened forming a concave spatula (Fig. 4a). The concave side points to the surface of the cuticula. Besides these hairs the femur, tibia and the tarsi bear long pointed bristles with a



Figs. 3–4. 3, Chitinous odour ducts (with a diameter of ca. 2 μm). 3a, on the inner side of tergite I of *X. nigrocincta*; 3b, on the inner side of tergite II of *X. violacea*. 4, Hairs on the hind legs of male *X. bimaculata*. 4a, the widened and flattened tips form a concave spatula. 4b, hairs on the anterior side of the femur. 4c, hairs on the antero-ventral side of the tibia. Scale bars: 3a) 40 μm , 3b) 100 μm , 4a) 40 μm , 4b) 200 μm , 4c) 200 μm .

rough surface. On the femur the spatula-like hairs are directed rectangular to the long axis of the femur (Fig. 4b) whereas on the tibia they are directed parallel to its

long axis (Fig. 4c). The function of this position of the hairs on the hind leg becomes clear when we look at the behaviour of *X. bimaculata* males in their territories.

Territories.—The mating period of *X. bimaculata* is from early October until late November. Due to the high altitude of the study site there is only one mating period. Males were recorded to fly in their territories between 06:15 and 16:30, the minimum temperature was 18°C. Individual territorial flights lasted up to 1.5 hours.

The territories of these males were always found at the very margins of the araucaria forest in non-flowering trees or shrubs. The males established their territories always on the sunny side of the forests and shifted them according to the position of the sun. They flew in territories with a radius of ca. 30 cm, sited between twigs or close to a bough, always in the shadow, positioned between 0.5 and 4 meters above the ground. The males kept their head downwind and changed their direction (not the position) according to the wind. Marked males were found to occupy the same territory on different days. However, this was not the rule.

In 1995 we observed 167 territories, 74% of them as single territories, in 26% 2–4 males established territories in close vicinity in the same tree. In 1994 we found leks with up to 10 males. The number of males in a lek changed frequently often within a few minutes. Sometimes the distance between the territories measured only 50 cm.

Territorial behaviour.—Within their territories the males of *X. bimaculata* hovered with loud buzzing mostly at one position, only shifting the direction from time to time to stay with the abdomen in the upwind position or in search for approaching females. Sometimes a male moved to establish the territory in another place without any recognizable reason. Males that left their territory probably to feed returned to their former or to a different position. In about 5% of the observed territorial flights males landed on the substrate within the territories. However, we could never observe them to rub their mandibles, their abdomen or legs over the substrate. Some of these males which had

landed were observed to brush their legs over their body.

While on wing in their territory the males held their fore and middle legs close to the body, so that the shiny white hairs on the fore and middle leg basitarsalia directed downwind and forward. The hind legs were stretched out backwards and away from the body. With high frequency (up to 11 times per minute) the males brushed with their hind legs from anterior to posterior over the dorsilateral parts of the abdomen, bending the abdomen downwards. They then rubbed the hind legs to each other and then to their middle legs. Less frequently they rubbed the middle legs to the fore legs and rarely the fore legs to the head. Towards the end of the territorial flight the males carried out these brushing movements with an ever decreasing frequency.

During the observation of 167 territories not a single female approached a male in its territory.

Males of *X. bimaculata* regurgitated and dehydrated nectar while hovering in the territory.

Aggressions between males.—Males in neighbouring territories have sometimes been observed to suddenly attack their neighbour. Some incoming males attacked territorial males immediately or were attacked by the hovering male. Sometimes the defending male left the territory to fly towards the intruder and hovered in front of him until one of them started to show antagonistic behaviour, including hits with the front legs, tumbling down while clinging to each other or chasing the opponent until both got out of sight of the observer.

Finally one male returned to the former territorial position, or in some cases even both males started to hover in close vicinity. Aggressive behaviour could be artificially initiated when we approached a dead male closer than 30 cm to a territorial male.

Volatile substances in cuticular wash-

ings.—In cuticular washings from the dorsilateral parts of the abdomen we could determine a series of alkanes with a chain length of 18 and longer as well as alkenes with the same chain length.

DISCUSSION

Males of *X. bimaculata* were found to establish non-resource based territories, either alone or together with other males in leks. We could not observe that they mark substrate in their territories in order to attract females. Instead males were seen to brush their body with their legs. We suppose that while the hind legs brush over the abdomen they take up secretions of the odour glands and spread them during further movements over the plumose hairs over the abdomen and over the hind and middle legs. Good evidence for this is that the males bend their abdomen downwards and stretch it so that the pores of the odour glands are exposed. While the males move their hind legs over their abdomen femur and tibia are held in a 90° angle. The different exposition of the specialized hairs on femur and tibia ensures that they brush straight over the pores of glands. So the spatula-like tips can take up the secretions from the plumose hairs surrounding these pores and spread them subsequently over the long bristles on both sides of the abdomen and over the other legs. These movements and the high frequency with which they are carried out strongly suggest that the males perfume their body in order to attract conspecifics.

While the male is emitting these secretions he is facing downwind. This position possibly ensures that the male might see incoming females that follow an odour trace. The white areas in his face and the shiny white hairs on his middle and front legs could then serve as a further signal for approaching females to detect the male in its territory.

The chain length of the alkanes and alkenes we found in the cuticular washings suggests that they are not highly volatile.

Those substances may more likely serve as short range signals, maybe for mate acceptance in a female choice system or to detect the males at the margins of the forests. Further studies on the chemical properties of the gland secretions and their function during territorial and mating behaviour are necessary.

Unfortunately we could not observe copulations in *X. bimaculata*. Therefore, any further considerations on the function of the modified forelegs can only be hypothetical.

Anzenberger (1977) clearly observed that during copulation males of *X. (Mesotrichia) torrida* Westwood cover at least a part of the female's compound eyes with the fan of long bristles on their mid legs. Osten (1989) showed that in *Xylocopa* species from Africa and Sri Lanka such fans on fore legs also function as blind folds during copulation. These blind folds may have the effect that females stop flying when grabbed in mid air or prevent them to take off when mounted by a male on substrate.

The phenomenon that male Hymenoptera have blind folds and odour glands in modified forelegs was so far found in more than one hundred species of megachilid bees, in several species of neotropical and Old World carpenter bees and furthermore in a sphecid wasp (*Crabro cribrarius*) (Wittmann 1992, Wittmann and Blochtein 1995, Blochtein 1995).

Osten (1989) has described that during copula position in *X. perforator* males hold their basitarsi on the female's head. In these basitarsi Wittmann and Blochtein (1995) found odour glands. Combining both findings we strongly suggest that males during copula bring the secretions of the odour glands in close contact with the antennae of the female. Further students of *X. bimaculata* mating behaviour may therefore check whether such a copula position can also be found in these bees.

In contrary to male *X. nigrocincta*, which concentrate the nectar in the mother's nest

before each territorial flight (Wittmann and Scholz 1989), the males of *X. bimaculata* dehydrated nectar while hovering in the territory. We suppose that thereby male *X. bimaculata* improve their energy budget as has been shown for *X. nigrocincta*. While the latter are fed by their mother in the nest, the males of *X. bimaculata* collect the nectar by themselves and therefore have to evaporate the redundant water during the territorial flight.

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Load-lifting Constraints on Provisioning and Nest Building in the Carpenter Wasp, *Monobia quadridens* L. (Hymenoptera: Eumenidae)

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Abstract.—The foraging and mud-carrying capacity of the trap-nesting carpenter wasp, *Monobia quadridens* L., was examined in relation to load-lifting ability. The body mass of caterpillar prey collected increased over the course of the season. Consequently, the ability of the wasps to carry prey became compromised late in the season. Caterpillar mass was not correlated with wasp size, but the mass of mudballs used in nest construction was related to wasp size. Wasp foraging may be constrained by the size of pyralid caterpillars available at any particular time, which changes because of caterpillar growth. Mudballs are constructed by the wasps themselves; therefore, wasps may be able to optimize mudball size in accordance with their own size, but mudballs were much lighter than caterpillars and never approached the upper limit of the wasps' ability to carry them.

Optimal foraging theory suggests that an animal will experience increased fitness as it becomes more efficient at obtaining food or energy. One obstacle encountered by flying insects that carry food loads is the need to generate sufficient lift force to remain airborne. Prey selection may be limited by the size of the prey the insect can successfully carry while in flight. Marden (1987) demonstrated that maximum still-air lift force in flying animals depends primarily on flight muscle mass (M_{fm}). A fixed minimum ratio of flight muscle mass to total mass lifted, the marginal flight muscle ratio, is required for successful takeoff. Animals with higher flight muscle ratios (FMR) have greater maneuverability, and should be better able to lift and carry loads, seize prey, avoid predators and vie for territories and mates (Marden 1987).

Recent studies examining the relationship between maximum lift force and actual load carriage in foraging and provisioning wasps have used ground-nesting species, including *Vespula* spp. (Coelho and Hoagland 1995), *Sphecius speciosus*

Drury (Coelho 1997), and *Sphex ichneumoneus* L. (Coelho and LaDage 1999). In the present study we investigate load carriage during provisioning and mud-carrying in *Monobia quadridens* L. (Hymenoptera: Eumenidae), an aerial nester.

Aerial nesting may apply additional constraints to load carriage. Two ground nesting species, the cicada killer (*Sphecius speciosus*) and the great golden digger wasp (*Sphex ichneumoneus*) are able to carry heavier loads than are theoretically possible, primarily by climbing vegetation, then flying toward their burrows (Coelho 1997, Coelho and LaDage 1999). Although presumably using maximum power, such overloaded wasps can only descend. Aerial nesters lack this option, as the final flight to the nest requires a vertical takeoff and ascent to the nest entrance. *M. quadridens* may not attempt to carry near-maximal loads if the load compromises flight maneuverability and nest entry.

The carpenter wasp, *M. quadridens*, readily nests in old borings of carpenter bees, *Xylocopa* spp. (Tandy 1908, Rau 1935), and

is the largest vespoid wasp to use wood trap-nests (Krombein 1967). A mature female removes debris inside the nest cavity and collects mudballs by moistening soil with water stored in the wasp's crop (Spradbery 1973) or with saliva (Evans and Eberhard 1970). Mudballs are used to construct the nest's interior plug, cellular partitions and exterior plug. Prior to mass provisioning with paralyzed caterpillar prey, a female deposits an egg near the inner end of the cell (Krombein 1967, Spradbery 1973). A partition is constructed between cells. A vacant space, the vestibular cell, is made near the nest's opening and sealed with a thick exterior plug. *Monobia quadridens* takes four to seven days to provision a nest (Krombein 1967).

The larva emerges 5 to 8 days after the egg is laid, feeds on the paralyzed caterpillars, applies a varnish to the cell's interior and pupates. The elapsed time between pupation and adult emergence averages 17 days for males and 18 days for females (Krombein 1967). Teneral adults remain inside their cells for 2 to 3 days while their integument and wings sclerotize, then chew through the cell partition to escape from the nest (Krombein 1967, Cowan 1991).

Monobia quadridens often provisions its nest with a single species of Lepidoptera; with pyralid caterpillars the most frequent. Stenomid and tortricid caterpillars were also used to provision nests (Krombein 1967). Female *M. quadridens* collecting long caterpillars, 10–18 mm, used fewer caterpillars per cell than those using prey that were only 6–13 mm in length (Krombein 1967). Theoretically, wasps carrying larger loads make fewer trips, thus conserving time and energy (Reavey 1993). The demands of temporal and energetic efficiency therefore interact with the constraints of load-lifting.

This study examines how load-lifting limitations influence the provisioning and mud-carrying strategies of *M. quadridens*. A female wasp should carry caterpillars

and mudballs that are near the maximum load-lifting capacity without exceeding it in order to save time and energy by reducing the number of trips. In other words, a female carrying prey or mudballs should have a FMR slightly above the marginal FMR for Hymenoptera, 0.179 (Marden 1987).

MATERIALS AND METHODS

Field research was conducted from June through September 1996, 1997 and 1998 at Alice L. Kibbe Life Science Station, Hancock County, Illinois. Observations and data collection were limited to sunny days because *M. quadridens* was not very active on overcast or rainy days.

M. quadridens females were nesting in abandoned carpenter bee holes in the wooden support beams beneath the upper level porch on the east side of the Frank House, a wooden frame building housing the field station's education center. To provide additional nesting sites for *M. quadridens*, artificial trap-nests were constructed according to Krombein (1967). A 12.7-mm diameter hole was drilled along the central longitudinal axis of straight-grain pine boards (38.1 mm × 38.1 mm × 200 mm) to a depth of approximately 152 mm. 12.7 mm dia holes adequately accommodate *M. quadridens* females' large size (Krombein 1967). Metal brackets held the traps in place on the faces of the support beams at two meters.

Initially, female wasps without prey were captured with an insect net and coaxed individually into a 1.5 ml microcentrifuge tube (ventilated by puncturing a hole in the lid) and placed in the refrigerator for 30 minutes. Wasps were marked on the dorsal side of the thorax with one or two small dots of enamel hobby paint. Special care was taken to avoid getting paint on antennae, wings or spiracles. Body mass (M_b) for each wasp was determined to the nearest 0.001 g on an Ohaus® electronic balance. The wasp was then placed outdoors near the nesting site and

allowed to recover fully and fly away. Individuals recaptured over the course of several days had M_b measured for each of those days.

Subsequent captures of marked females were made whenever they returned with a caterpillar or mudball. Wasp and caterpillar were collected and placed into a ventilated tube and unventilated tube, respectively. The caterpillar's body mass (M_{prey}) was determined to the nearest 0.001 g. Wasps returning with mudballs were also captured. Wasp and mudball were collected and placed into a ventilated tube and unventilated tube, respectively. Gentle handling of the mudballs was employed to prevent them from crumbling. The mudball's mass (M_{mud}) was determined to the nearest 0.001 g. In both situations, marked wasps were chilled, reweighed, and released as previously described. Multiple caterpillars and/or mudballs were often collected from a single individual. After a wasp arrived with its third (at most) caterpillar it was placed in an airtight tube and frozen. The number of mudballs collected before the wasp was taken was highly variable. For two individuals, both caterpillar and mudball data were obtained. Female wasps were frozen and transported to the laboratory for additional measurements. An Ohaus® analytical balance accurate to ± 0.0001 g was used to determine M_b for each female wasp. The head, abdomen, legs and wings were cut away and thorax mass (M_{th}) was measured. Because flight muscle composes 95% of thorax mass in Hymenoptera (Marden 1987), flight muscle ratio was calculated as $0.95M_{\text{th}}/M_b$. Operational (loaded) flight muscle ratio (FMR_o) was determined as $0.95M_{\text{th}}/(M_b + \text{mass of load carried})$. Voucher specimens were deposited in the Entomology Museum of Western Illinois University.

Average M_b and unloaded FMR were calculated for individual wasps that carried multiple caterpillars and/or mudballs. The individual averages were then

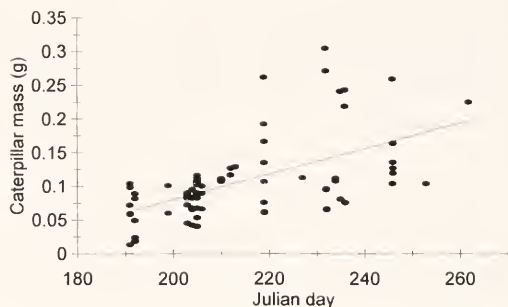


Fig. 1. The effect of time of year on body mass of caterpillars carried by *Monobia quadridens*.

used to determine all descriptive statistics for each of these categories to avoid pseudoreplication (Zar 1996). Statistical analyses were performed using Systat® 6.0 for Windows (SPSS Inc., Chicago, IL), Corel Quattro Pro® 6.02 for Windows (Corel Corp. Ltd.), and StatMost® (Datamost Corp.)

RESULTS

Data were collected on a total of 54 female *M. quadridens*: 10 from 1996, 24 from 1997 and 20 from 1998. Thirteen wasps returned more than once with loads prior to being sacrificed, thus sample sizes differ for prey, mudballs and total wasps. All prey carried by *M. quadridens* were in the family Pyralidae.

Regression analysis of M_{prey} on M_b for all wasps was not significant, nor was M_{prey} on M_{th} ($P > 0.05$). The average M_b was 0.2184 ± 0.0059 , $n = 54$. The smallest wasp (0.09 g) was observed hauling two caterpillars simultaneously with a total prey mass of 0.104 g. This load was almost identical to the average load carried by a female nearly three times the size of the smallest wasp.

Caterpillar body mass increased over the course of the season and was linearly related to Julian day ($M_{\text{prey}} = -0.299 + 0.0019\text{day}$, $n = 74$, $R^2 = 0.316$, $F = 33.3$, $p < 0.0001$) (Figure 1). Late-season caterpillars were nearly double the M_b of those taken during June and July.

Increasing caterpillar size affected the

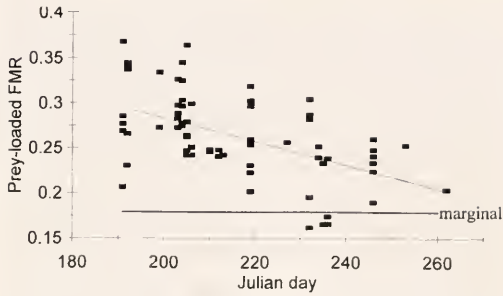


Fig. 2. The effect of time of year on operational (prey-loaded) flight muscle ratio in wasps carrying caterpillars. The marginal level indicates the minimum flight muscle ratio required for successful take-off.

prey loaded FMR_o (0.2633 ± 0.0054 , $n = 71$), which decreased significantly over the course of the season ($FMR_o = 0.544 - 0.0131\text{day}$, $n = 71$, $R^2 = 0.267$, $F = 25.1$, $p < 0.0001$) (Figure 2). Late in the season, the increase in prey mass caused the loaded FMRs to fall below the marginal FMR for Hymenoptera.

In four of 71 (5.6%) foraging events, the wasp had an average loaded FMR below the marginal FMR (Figure 3). Each of these individuals carried large caterpillars weighing an average of 0.252 g. This mass was 233% greater than the overall mean M_{prey} (0.108 g). No early-season, prey-laden wasp approached the marginal FMR for Hymenoptera.

As wasp size increased, the size of mudballs (mean = 0.0513 ± 0.0032 g) used during nest construction increased. Significant relationships demonstrated the effect of wasp mass on mudball mass: M_b versus M_{mud} ($M_{\text{mud}} = 0.0051 + 0.1943M_b$, $n = 38$, $R^2 = 0.270$, $F = 13.3$, $p = 0.0008$) (Figure 4). A weaker, but significant effect of M_{th} on M_{mud} was also present ($M_{\text{mud}} = -0.0054 + 0.6072M_{\text{th}}$, $n = 27$, $R^2 = 0.205$, $F = 6.44$, $p = 0.018$).

The average mudball mass was 50% less than and significantly different from ($t = 7.36$, $df = 99$, $p < 0.0001$, t -test) the average prey mass ($0.1081 \text{ g} \pm 0.0069$, $n = 74$). Consequently, the mean FMR for females

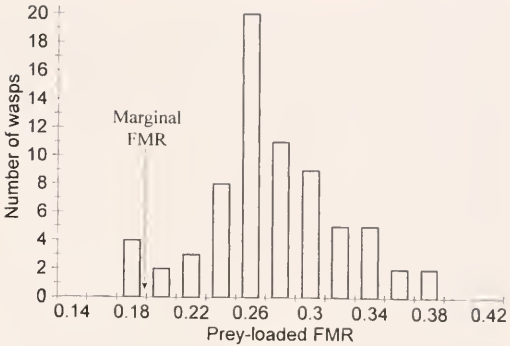


Fig. 3. The distribution of operational flight muscle ratios among wasps carrying caterpillars. The marginal level indicates the minimum flight muscle ratio required for successful take-off.

loaded with mudballs, (0.3099 ± 0.0033 , $n = 27$) was well above the marginal FMR.

DISCUSSION

Wasp body mass and thorax mass did not affect the size of prey provisioned. If females were actively selecting prey by size, they should take the largest caterpillars they can lift. Thus, larger wasps would be choosing larger prey, as occurs in *S. ichneumonaeus* (Coelho and LaDage 1999) and *Palmodes laeviventris* Cresson (Gwynne and Dodson 1983). Females would spend less time foraging and energy would be conserved. However, observations of *M. quadridens* did not support this hypothesis.

As the season progressed, caterpillar

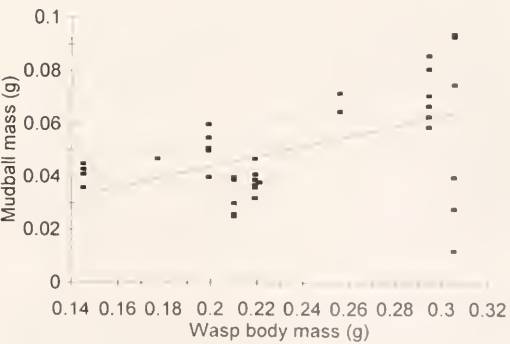


Fig. 4. The effect of wasp body mass on mass of mudballs carried by *Monobia quadridens*.

size increased, consequently decreasing the FMR_0 of foraging wasps. Early in the season, females exhibited no difficulty in carrying prey. Prey mass was never large enough to substantially decrease the FMR_0 ; therefore, loaded females remained well above the marginal FMR for Hymenoptera. In August, however, provisioning females encountered load-lifting constraints because of the increasingly large caterpillars. As a result, the FMR of loaded individuals dropped near or slightly below the marginal FMR.

Considering the prey cues available to predatory wasps and their acute visual abilities, it is doubtful that early in the season *M. quadridens* females would be incapable of finding larger caterpillars if such prey were present (Stamp and Wilkens 1993). It is more likely that females provisioned smaller prey at this time because they were the most readily available, if not the only suitable prey available.

In early summer, females, regardless of individual size, primarily foraged on small-bodied caterpillars. Caterpillars presumably grew as the summer progressed, and late in the season *M. quadridens* females were not always successful in their attempts to carry the larger caterpillars. On one occasion a female made no attempt to recover a large caterpillar after dropping it. Another low-flying wasp fell to the ground without dropping the prey item, crawled 30 cm up a beam then flew 183 cm (horizontal flight) and landed on a chair. Again, she tumbled to the ground and dragged the caterpillar 147 cm through the grass prior to abandoning it. These two late season caterpillars had an average mass of 0.256 g, which was twice the size of the largest early season caterpillar. As a result, individual FMR_0 fell to between 0.239 and 0.165, and caterpillars were dropped.

Typically, predators choose prey that are large enough to make it worth their time and energy, yet small enough to be easily carried (Reavey 1993). The loss of

time and energy resulting from failed foraging attempts on large caterpillars suggests that either small caterpillars were in short supply, or that success was frequent enough to outweigh failure. Indeed, on occasion females successfully brought in prey larger than themselves. In one case, a female was loaded with a caterpillar 1.5 times greater than her own body mass.

Similar effects of changing prey size because of prey growth are known from other species. Seasonal variation in caterpillar size also dramatically affects the provisioning style of the solitary digger wasp *Ammophila sabulosa* L. (Field 1992). Large prey are taken more frequently during the second part of the nesting period (entire nesting period runs from late June through early September) and are carried on foot. Early in the season, when smaller prey are more common, provisioning wasps require a greater number of small prey, which they carry in flight. Furthermore, smaller wasps multiply-provision their nests (using smaller prey) more frequently than larger wasps (Field 1992).

Brockman and Grafen (1992) describe the effect of the growth of spiders on their predator, the mud-dauber, *Trypoxylon politum* Say. At the start of the season, wasps forage on a genus of spiders (*Eustala*) that overwinter as adults. The majority of the season, wasps provision with the genus *Neoscona*, which overwinter as spiderlings. As spider size gradually increases, wasps late in the season experience difficulty hauling the larger spiders, frequently dropping them. Additionally, wasps expend more energy and risk being attacked by large adult spiders. Landes et al. (1987) found that "wasps collected spiders in numbers relative to their seasonal and relative abundance, accessibility as prey, or size suitability."

In addition to carrying caterpillar prey, female *M. quadridens* also carried mudballs used in nest construction. Wasp body mass significantly influenced the mass of mudballs carried. This effect sug-

gests that females constructed mudballs of a size proportional to their individual body size. These findings are consistent with Archer's (1977) study of *Paravespula vulgaris* (L.), in which forager body size was significantly correlated to the earthen load carried by wasps leaving the nest.

In contrast to several of the prey-loaded FMRs that dropped below the marginal FMR, females never carried mudballs large enough to substantially decrease their FMR_{mud} . The FMR_{mud} values were far greater than the marginal FMR. *M. quadridens* may not optimize energy costs of mudball production and carriage because of the style used to carry mudballs. Wasps may be restricted to making small, round mudballs compact enough to be easily carried in their mandibles. The difference in carriage style between prey and mud perhaps best explains why female *M. quadridens* could haul heavier prey loads than mudballs. Caterpillars were grasped with all legs and held lengthwise against the female's underside without altering the center of gravity (Evans 1962). In contrast, mudballs carried with the mandibles and forelegs placed additional weight toward the head, altering balance. To compensate, individuals may have been restricted to hauling mudballs that were much lighter than the prey.

On average, *M. quadridens*' unloaded FMR (0.385), although higher than the mean for Hymenoptera (0.34 ± 0.013 , $n = 15$; data from Marden 1987, Coelho 1991, 1997, Coelho & Hoagland 1995, Coelho and LaDage 1999), is similar to that of other vespoids such as *Vespula* (Coelho and Hoagland 1995). *M. quadridens*' FMR was considerably lower than that of the ground-nesting sphecids *Sphecius speciosus* (0.416, Coelho 1997) and *Spheg ichneumoneus* (0.462, Coelho and LaDage 1999). *M. quadridens* is therefore less maneuverable than the ground nesters when unladen. However, the mass allocation of *M. quadridens* should be matched to the maximum demands of load carriage, which occur

when prey are carried. Only 5.6% of provisioning events caused *M. quadridens* to have an FMR_0 below marginal. In contrast, *Sphecius speciosus* and *Spheg ichneumoneus* provision at levels below marginal FMR_0 90% (Coelho 1997) and 25% (Coelho and LaDage 1999) of the time, respectively. Therefore, *M. quadridens* is on average more maneuverable when provisioning than the ground nesters. Aerial nesting may, in fact, carry maneuverability restrictions as predicted.

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Reproductive Biology of the Seed-harvester Ants *Messor julianus* (Pergande) and *Messor pergandei* (Mayr) (Hymenoptera: Formicidae) in Baja California, Mexico

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Abstract.—The seed-harvester ant *Messor julianus* (Pergande) exhibits a parapatric distribution pattern with the ecologically equivalent congener *M. pergandei* (Mayr) in the Baja California peninsula of Mexico; *M. pergandei* replaces *M. julianus* in drier soil microhabitats within the contact zone between these two species. This paper describes the reproductive biology of *M. julianus* and *M. pergandei* to provide a first step in understanding factors involved in causing this replacement pattern. Mating flights of *M. julianus* were observed over a several week period from early February to early March, and thus appear similar to those of *M. pergandei*. Likewise, starting nests of both species contained one foundress. Moreover, the similar ecology and mating flights of *M. julianus* and *M. pergandei* suggest that the replacement pattern exhibited by these two species is associated with patterns of foundress survival. In regard to mating flights, both *M. julianus* and *M. pergandei* are postulated to have diverged from the putative ancestral condition of summer mating flights that occur in other Nearctic congeners. This seasonal difference in timing of the mating flight for these two species correlates with their being the only Nearctic species of *Messor* that are restricted to hot desert habitats. Alate females for both *M. julianus* and *M. pergandei* have poor tolerance to high temperature relative to desert ants in the genera *Aphaenogaster* and *Pogonomyrmex*.

The seed-harvesting ant genus *Messor* (Hymenoptera: Myrmicinae) is common throughout the southwestern deserts of the United States and northwestern Mexico. Four species of *Messor*, *M. andrei* (Mayr), *M. julianus* (Pergande), *M. pergandei* (Mayr), and *M. stoddardi* (Emery), occur in the Baja California peninsula of Mexico; *M. julianus* is endemic to the peninsula (Johnson 2000a; R. Johnson and P. Ward, unpubl. data) (Fig. 1). Two of these species, *M. julianus* and *M. pergandei*, are common in most low elevation habitats (< ≈1000 m) with their combined geographic distributions encompassing all but the northwest portion of the peninsula. The other two species, *M. andrei* and *M. stoddardi*, are largely restricted to coastal and adjacent inland areas along the Pacific Coast. In the Baja California peninsula, *M. andrei* is restricted to the relatively mesic

California Floristic province in the northwest portion of the peninsula (R. Johnson and P. Ward, unpubl. data). The range of *M. stoddardi* extends to central portions of the peninsula, but this species rarely coexists with *M. julianus* or *M. pergandei* (R. Snelling, unpubl. data; R. Johnson, pers. obs.) (Fig. 1).

Messor julianus and *M. pergandei* are ecologically similar species. Colonies of both species consist of many thousands of workers that forage in long columns (Johnson 2000a), and these two species are the only Nearctic *Messor* that are restricted to occurring in hot desert habitats (Wheeler and Wheeler 1973). Geographically, *M. julianus* is mostly restricted to central and southern portions of the peninsula, while *M. pergandei* occurs in eastern portions of the peninsula to as far south as northeastern BCS (the state of Baja California Sur)

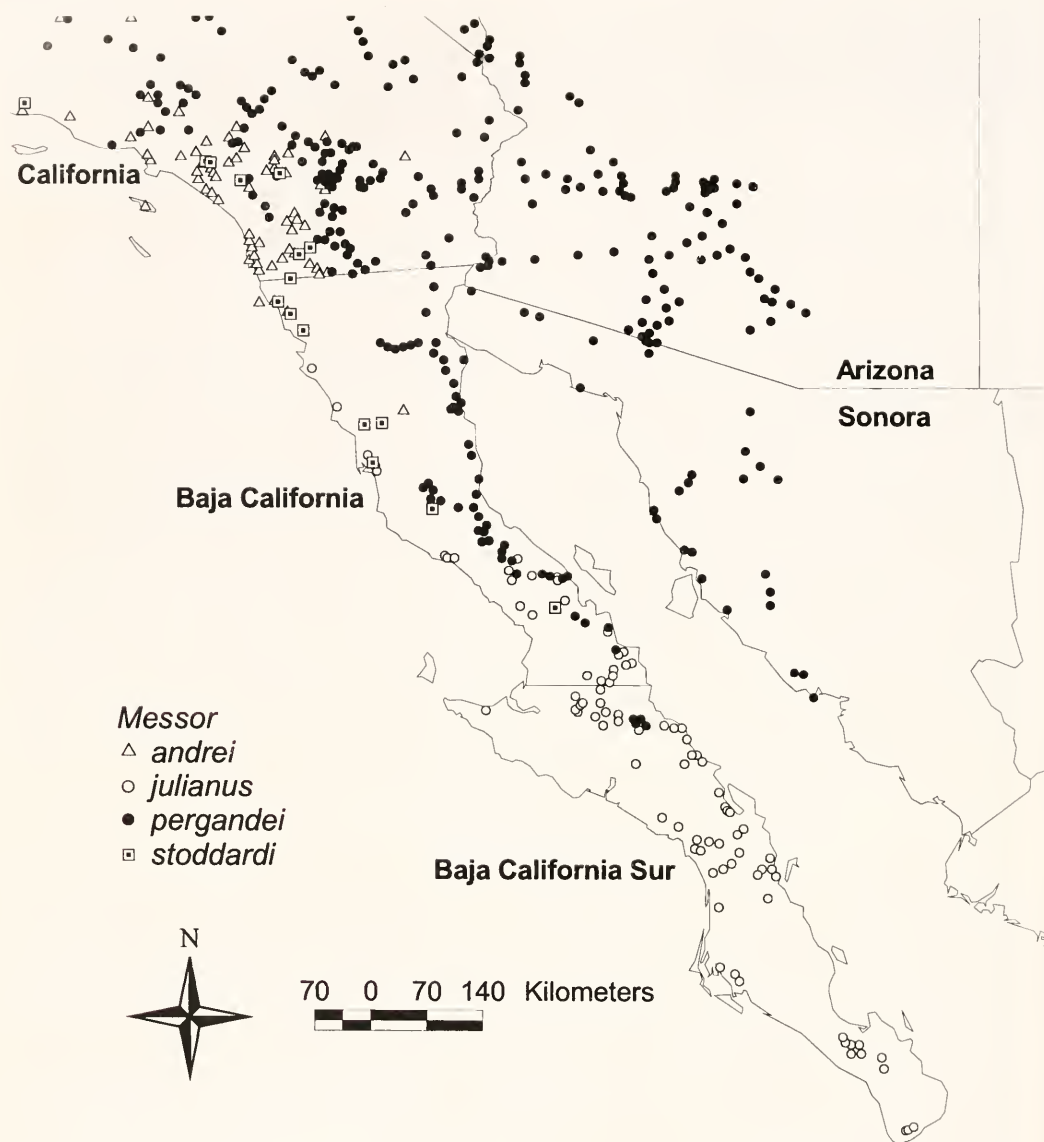


Fig. 1. Geographic distribution of species of *Messor* that occur in the Baja California peninsula, Mexico. The full geographic distribution of each species is given in Johnson (2000a).

(Fig. 1). In northern and central BC (the state of Baja California), *M. julianus* inhabits a narrow range along the cool Pacific Coast, while *M. pergandei* is restricted to xeric desert areas along the eastern coast. Moreover, these two species exhibit a parapatric distribution pattern (herein defined as species that occupy separate but adjoining areas, such that only a small

fraction of individuals in each encounters the other [Futuyma and Mayer 1980]) with ranges of the two species overlapping across a contact zone in the central peninsula (Fig. 1). While the two species are often sympatric within the contact zone, the pattern across the contact zone is one in which the two species replace one another along local gradients that correlate

with abiotic habitat features (Johnson 2000a). Across the contact zone, *M. pergandei* inhabits the drier microhabitats, i.e., those that are lower in elevation or in which the soils have a higher percentage composition of sand (drier soils) (R. Johnson, pers. obs.).

Colony founding is the most vulnerable stage in the life history of ants (Tschinkel 1992, Herbers 1993, Johnson 1998), and it is this stage that likely determines micro- and macro-distribution of adult colonies. Thus, comparative data on reproductive biology of *M. julianus* and *M. pergandei* provide a first step in understanding factors involved in causing the replacement pattern exhibited by these two species. Mating flights of *M. pergandei* are well known and typically occur between late January and mid-March (Pollock and Rissing 1985, Ryti 1988, Cahan *et al.* 1998), and thus deviate seasonally from the summer mating flights of other Nearctic *Messor* (Creighton 1953, Cole 1963, McCluskey 1963, Wheeler and Wheeler 1973, Snelling and George 1979, Brown 1999, R. Snelling, unpubl. data, M. Bennett, pers. comm.). In contrast, the mating flights and the female sexuals of *M. julianus* are undescribed in the literature. Based on the fact that *M. julianus* and *M. pergandei* are the only Nearctic *Messor* that are restricted to hot desert habitats, I hypothesized that the seasonal timing of mating flights was similar for these two species. I assessed potential physiological constraints on mating flight season by comparing high temperature tolerance for alate females of *Messor*, *Aphaenogaster*, and *Pogonomyrmex*.

METHODS

I observed ten colonies of *M. julianus* over nine days in mid-February 1993, near Highway 1 at 26 km northwest of Santa Rosalía, BCS (27°23'N, 112°28'W). All ten colonies had large nests and an active foraging column. The site was a sandy plain dominated by *Larrea tridentata*, *Opuntia cholla*, and *Pachycereus pringlei*. Through-

out the flight period each day, alates flying from nests were counted during sequential 2 minute visits to each nest. Ambient temperature was measured periodically about 5 cm above ground using a thermocouple thermometer.

The number of foundresses per starting colony was determined by excavating founding nests of *M. julianus* and *M. pergandei*. Data for *M. julianus* were collected 17–18 km west of La Purísima, BCS, (26°09'N, 112°13'W) in March 1992, and near Punta San Hipolito, BCS, (27°00'N, 114°00'W) in February 1998. These same data were collected for *M. pergandei* near Highway 1 at 17.5 km west of Bahía de los Angeles, BC, (28°59'N, 113°44'W) and along Highway 1 at 6 km south of the paved turnoff to Bahía de los Angeles, BC, (29°00'N, 114°10'W) in February 1995.

I assessed relative tolerance to high temperature by comparing survival for alate females of *M. julianus* and *M. pergandei* with that of two species of *Aphaenogaster* (*A. albisetosa* and *A. cockerelli*) and four species of *Pogonomyrmex* (*P. barbatus*, *P. occidentalis*, *P. rugosus*, and *P. salinus*) (see Table 1 for collection data); mating flights of both species of *Aphaenogaster* and all four species of *Pogonomyrmex* are triggered by summer rains (Johnson 2000a). Trials used test tubes that were partially filled with water trapped by cotton plugs. Alate females were placed into the tubes and the openings were plugged with moist cotton, thus providing *ad libitum* water at both ends. Trials at each temperature used one tube containing 25 individuals of one species that had been collected from at least four colonies. A separate set of individuals was used at each temperature. Each species was tested over 1° C increments that resulted in mortality ranging from 0–100%. The tubes were placed in a darkened incubator for 2 hours at the appropriate temperature; individuals unable to right themselves after that time were considered dead. Mortality data were compared among congeners and

Table 1. Collection data for alate females used in temperature tolerance tests. Localities are in the United States except as noted.

Species	Collection Locale	Latitude	Longitude	Elevation (m)	Collection Date
<i>Aphaenogaster</i>					
<i>A. albisetosa</i> Mayr	AZ: Pinal Co., 8 km NE Casa Grande	32°56'N	111°42'W	430	26 JUL 1995
<i>A. cockerelli</i> André	NM: Hildago Co., Jct. Hwys 9 & 80	31°56'N	109°02'W	1260	16 JUL 1994
<i>Messor</i>					
<i>M. julianus</i> (Pergande)	MEXICO: Baja California, 47.5 km S Bahía de los Angeles	28°38'N	113°20'W	80	3 FEB 1995
<i>M. pergandei</i> (Mayr)	MEXICO: Baja California, 29 km S Bahía de los Angeles	28°41'N	113°26'W	105	4 FEB 1995
<i>Pogonomyrmex</i>					
<i>P. barbatus</i> (Smith)	NM: Hildago Co., 3 km N Rodeo	31°52'N	109°02'W	1225	5 JUL 1993
<i>P. occidentalis</i> (Cresson)	AZ: Yavapai Co., Chino Valley	34°46'N	112°27'W	1450	30 JUL 1995
<i>P. rugosus</i> Emery	NM: Hildago Co., Jct. Hwys 9 & 80	31°56'N	109°02'W	1260	5 JUL 1993
<i>P. salinus</i> Olsen	NV: Clark Co., Dry Lake	35°54'N	114°56'W	520	30 AUG 1993

across genera using a contingency table analysis. For across genera comparisons, data sometimes were not available for temperatures below or above those causing 0 and 100% mortality. To make these comparisons, I assumed that the upper and lower bounds were threshold temperatures.

Voucher specimens are deposited at the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, the Los Angeles County Museum of Natural History, Los Angeles, California, and the Robert A. Johnson collection, Tempe, Arizona.

RESULTS

I observed mating flights of *M. julianus* from early February to early March. At the site northwest of Santa Rosalía, BCS, alates flew from 6 of the 10 observation colonies, with few alates released each day. Flights occurred on 4 of 9 days and were relatively synchronous among colonies, i.e., on a given day, alates either flew from several colonies or none of the colo-

nies (Figure 2). Mating flights typically occurred from 0830–1000 h (MST) at temperatures of 16–23° C. Flights occurred irrespective of mild breezes or overcast skies, but were precluded by light rain or moderate breezes. Alates temporarily retreated into nests following gusts of wind. After the last day, I excavated the ten observation colonies and several adjacent colonies. In all colonies, alates were present in very low numbers or absent.

Mating flights of *M. julianus* were also observed on 5 March, 1992, at 17 km west of La Purísima, BCS, (26°09'N, 112°13'W) and on 5 February, 1995, at 48.7 km south of Bahía de los Angeles, BC (28°38'N, 113°20'W). At the latter site, ten marked colonies of *M. julianus* were observed on 31 January and 5 February. On 31 January, no alates were observed outside any of the ten colonies and no foundresses were located at the site. On 5 February, alates were observed outside 6 of the 10 colonies and individuals flew from one of these nests and from several unmarked nests. Mating flights of *M. pergandei* were ob-

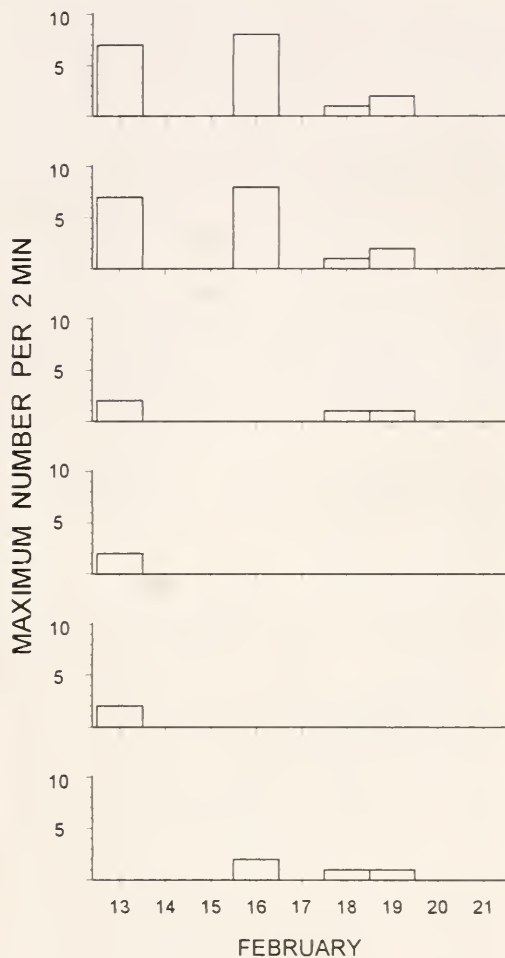


Fig. 2. Flight activity for six colonies of *Messor julianus* northwest of Santa Rosalía, Baja California Sur, Mexico, during February 1993. For each day, data are from the two minute observation period in which the highest number of alates were released from the nest.

served on 26 February, 1991, at Punta Estrella, BC, (30°55'N, 114°43'W) on 29 February, 1992, along Highway 1 at 16.0 km east of San Ignacio, BCS, (27°20'N, 112°46'W) and on 1–2 February, 1995, along Highway 1 at 17.5 km west of Bahía de los Angeles, BC (28°59'N, 113°44'W). The latter site had been visited several days earlier, but no foundresses of *M. pergandei* were located. All of 44 and 127 starting nests for *M. julianus* and *M. pergandei*, respectively, contained one foundress (Table 2).

Tolerance to high temperature was first compared between congeners. Species within all three genera had similar tolerance to high temperature (Chi-square, $P > 0.10$), so data for species within each genus were pooled. In contrast, tolerance to high temperature varied significantly across genera (Chi-square = 231.9, 14 df, $P < 0.001$). Subsequent between-genus tests demonstrated that temperature tolerance differed between *Messor* and both *Aphaenogaster* (Chi-square = 34.9, 5 df, $P < 0.001$) and *Pogonomyrmex* (Chi-square = 181.3, 7 df, $P < 0.001$). The primary contributors to Chi-square values were at low temperatures, where mortality was higher than expected for *Messor* and lower than expected for *Aphaenogaster* and *Pogonomyrmex* (Table 3). Overall, most individuals survived to 42–43° C in *Messor*, 44–45° C in *Aphaenogaster*, and 46–47° C in *Pogonomyrmex*.

DISCUSSION

Reproductive biology of *M. julianus* appears similar to that of *M. pergandei*. The asynchronous late winter to early spring mating flights of both species appear cued by photoperiod (McCluskey 1963) and extend for several weeks both within and among nests (Pollock and Rissing 1985). Mating flights of *M. julianus* were observed from early February through early March, and anecdotal observations suggest that most alates were released during this several week period. For example, at one site alates were observed outside of nests in early February but not several days earlier, which suggests that this was near the beginning of the mating flight season. Similarly, few if any alates could be excavated from nests after late February, suggesting the end of the mating flight season.

Mating flights of *M. pergandei* occur from early to mid-morning under clear skies as air temperatures reach about 22° C. The lower temperatures at which *M. julianus* initiates mating flights are associat-

Table 2. Number of foundresses in starting nests of *Messor julianus* and *M. pergandei* in the Baja California peninsula, Mexico. For location, BC = Baja California; BCS = Baja California Sur.

Species	Foundress Association Size		Location	Latitude	Longitude	Elevation (m)	Date
	1	>1					
<i>M. julianus</i>	40	0	17–18 km W La Purísima, BCS	26°09'N	112°13'W	100	4–5 MAR 1992
	4	0	Punta San Hipolito, BCS	26°58'N	113°59'W	5	10 FEB 1998
Total	44	0					
<i>M. pergandei</i>	23	0	Punta Estrella, BC	30°55'N	114°43'W	5	25–27 FEB 1991
	51	0	Highway 1 at 17.5 km W of Bahía de los Angeles, BC	28°59'N	113°44'W	80	3 FEB 1995
	53	0	Highway 1 at 6 km S of turnoff to Bahía de los Angeles, BC	29°00'N	114°10'W	365	3 FEB 1995
Total	127	0					

ed with this species also foraging at much lower temperatures. During winter and spring, foraging columns of *M. julianus* form prior to dusk and foraging continues into the night until ground temperatures decrease to $< 11^{\circ}\text{C}$ (R. Johnson, unpubl. data). Conversely, *M. pergandei* forages diurnally during this season, beginning after ground temperatures reach about 18°C (Bernstein 1974). While flights of *M. pergandei* are often precluded by overcast weather or slight breezes (Pollock and Rissing 1985), those of *M. julianus* often

proceeded, at least at low levels, under these conditions.

Both *M. pergandei* and *M. julianus* are haplometrotic (one foundress per starting nest) in the Baja California peninsula. In *M. pergandei*, the number of foundresses varies geographically from haplometrosis in southern California to pleometrosis (multiple foundresses per starting nest) in southeastern California and Arizona (Pollock and Rissing 1985; Rytí 1988; Cahan *et al.* 1998; Rissing *et al.* 2000). However, mature colonies of *M. pergandei* have a single

Table 3. High temperature tolerance ($^{\circ}\text{C}$) for alate females in the ant genera *Aphaenogaster*, *Messor*, and *Pogonomyrmex*. Values are per cent mortality for 25 individuals over 2 h with *ad libitum* moisture.

Species	Temperature ($^{\circ}\text{C}$)								
	40	41	42	43	44	45	46	47	48
<i>A. albisetosa</i>			0.0	0.0	48.0	80.0	100.0		
<i>A. cockerelli</i>		0.0	0.0	4.0	44.0	100.0	100.0		
<i>M. julianus</i>			0.0	72.0	100.0	100.0			
<i>M. pergandei</i>	0.0	4.0	4.0	88.0	100.0	100.0	100.0		
<i>P. barbatus</i>					0.0	0.0	0.0	44.0	100.0
<i>P. occidentalis</i>						0.0	12.0	100.0	100.0
<i>P. rugosus</i>					0.0	2.0	0.0	48.0	100.0
<i>P. salinus</i>						0.0	0.0	80.0	100.0

queen regardless of the initial founding strategy (Rissing and Pollock 1987; S. Rissing and J. Parker, unpubl. data). These data extend the distribution of haplometrosis for *M. pergandei* from southeastern California to its southern range limit in the Baja California peninsula such that both *M. pergandei* and *M. julianus* are haplometrotic where the two species are sympatric. Mating occurs in the air for *M. pergandei* (S. Rissing, pers. comm.) and *M. andrei* (R. Johnson, pers. obs.), with *in copulo* pairs of both species sometimes falling to the ground; mating in *M. julianus* is probably similar.

The replacement pattern exhibited by *M. julianus* and *M. pergandei* is common among seed-harvester ants in western North America (Johnson 2000a). For example, the ecologically equivalent species *Pogonomyrmex barbatus* and *P. rugosus* segregate microhabitats along gradients of soil texture. Foundresses of *P. rugosus* have a higher tolerance to desiccating conditions, which correlates with this species occurring in drier soil microhabitats (Johnson 2000b). The similar ecology and mating flights of *M. julianus* and *M. pergandei* suggest that the micro- and macro-habitat differences exhibited by these two species are also associated with patterns of foundress survival. Given that *M. pergandei* inhabits the more xeric micro- and macrohabitats, it is predicted that foundresses of this species are more desiccation tolerant than are foundresses of *M. julianus* (Johnson 2000a).

The late winter to early spring mating flights of *M. julianus* and *M. pergandei* are correlated with these being the only two Nearctic *Messor* that are restricted to hot desert habitats (Wheeler and Wheeler 1973). However, it is difficult to determine the sequence of character-state change in timing of the mating flight within Nearctic *Messor* because the phylogenetic relationships of this species group are unclear. *Messor* is a predominantly Old World genus, with the Nearctic components pre-

sumably having invaded North America from Asia via Beringia (R. Snelling, pers. comm.). Alternatively, some recent evidence suggests that the *Aphaenogaster* species belonging to the former *Novomessor* (including *A. albisetosa* and *A. cockerelli*) are the sister group to Nearctic *Messor* (Bennett 2000). Moreover, evaluating the ancestral mating flight condition depends upon determining the appropriate outgroup. The relationship between *M. julianus* and *M. pergandei* is also poorly resolved (Bennett 2000) because the clade containing these two species also contains *M. lariversi*, which is a Great Basin species that has summer mating flights.

One possible evolutionary scenario is the late winter to early spring flights evolved one time and are common by descent in *M. pergandei* and *M. julianus*. If this is the case, the shift from a summer to a late winter to early spring flight season may have been necessitated by physiological constraints related to temperature tolerance, and prerequisite to these two species invading hot desert habitats. Moreover, alate females of both species have poor heat tolerance compared to species of *Aphaenogaster* and *Pogonomyrmex*, suggesting *Messor* foundresses could not survive soil temperatures present during summer. A similar temperature constraint occurs in the desert leaf-cutter ant *Acromyrmex versicolor*, whose mating flights are triggered by late summer rains. Females of *A. versicolor* also have poor tolerance to high temperature, and the foundresses survive by selectively initiating nests in shaded, cooler microhabitats (Rissing *et al.* 1986).

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Morphofunctional Adaptations of Parasitoids Attacking Concealed Eggs of Two Arboreal Mirids in Italy

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Abstract.—The morphofunctional adaptations of the egg parasitoids of two arboreal mirids (Heteroptera: Miridae) for reaching the concealed eggs of their hosts, *Calocoris quadripunctatus* (Villers) and *Calocoris trivialis* (Costa), were studied in a natural ecosystem (oak forest) and in an agroecosystem (orange groves), respectively. *Calocoris quadripunctatus* is a predator of immature stages of *Tortrix viridana* (L.) (Lepidoptera: Tortricidae) in deciduous oak forests, *Quercus* spp., in Tuscany. Eggs are laid in clusters and concealed among the scales of dead buds, where they are exploited by two parasitoid species. *Chaetostricha walkeri* (Förster) (Hymenoptera: Trichogrammatidae) has a long ovipositor which is inserted between the scales to reach the host eggs, and is therefore an "ovipositor prober". Instead, *Telenomus* sp. *laricis* Walker group (Hymenoptera: Scelionidae) has a depressed metasoma which is introduced between the scales, and is therefore a "metasomal prober". *Calocoris trivialis* is a phytophagous species that damages orange groves, *Citrus sinensis* (L.), and other *Citrus* spp. in Sicily. The eggs are concealed in the soft, decaying wood of old pruning wounds and are attacked by at least two parasitoids. *Aprostocetus* n. sp. near *miridivorus* (Domenichini) (Hymenoptera: Eulophidae) is probably both an "ovipositor prober" and an "ovipositor driller", as it can also drill through the wood. *Telenomus lopicida* Silvestri (Hymenoptera: Scelionidae) has a long ovipositor and a compressed metasoma, which is introduced into the host incision, and is therefore a "metasomal prober". Such morphological adaptations appear to be linked to the host oviposition sites and explain some aspects of parasitoid exploitation efficiency; they may also help interpret other host-parasitoid associations that are unknown or questionable.

Mirid bugs (Heteroptera: Miridae), the largest family of Heteroptera, are very common both in arboreal and herbaceous ecosystems, where they feed on plants (phytophagous species), other arthropods (zoophagous) or both (zoophytophagous) (Wagner and Weber 1964, Alomar and Wiedenmann 1996). Their eggs are elongated with a true operculum on their anterior pole and are more or less deeply embedded in dead or living plant tissues, or concealed between plant organs (Kullenberg 1946, Southwood 1956, Cobben 1968, Hinton 1981). In spite of these kinds of protection, mirid eggs can be attacked by parasitoids belonging to Eulophidae, Trichogrammatidae, Scelionidae and My-

maridae (Hymenoptera) (Bin and Vinson unpublished). Some of these host-parasitoid associations from a natural ecosystem, oak forest, in Tuscany (central Italy) and from an agroecosystem, orange groves, in Sicily (southern Italy), are described here, focusing on morphological features related to parasitoid strategies.

Oaks in Tuscany are attacked by *Tortrix viridana* (L.) (Lepidoptera: Tortricidae), which is distributed over large portions of the Palearctic region, from northern Europe to the Mediterranean region, and during population outbreaks can seriously defoliate vast groves (Bogenschütz 1978). Eggs and possibly young larvae of this tortricid are preyed upon (Roversi unpub-

lished) by the zoophytophagous mirid *Calocoris quadripunctatus* (Villers) (Wagner and Weber 1964), the population size of which was found to be directly dependent on *T. viridana* density (Roversi *et al.* in preparation). *Calocoris quadripunctatus* has one generation per year and overwinters in the egg stage. Eggs are concealed in dead buds, between external scales that are partially spaced out, where they are attacked by *Chaetostricha walkeri* Förster (Hymenoptera: Trichogrammatidae) and a *Telenomus* sp. (Hymenoptera: Scelionidae) (Conti *et al.* 1997, Roversi *et al.* 1998) which belongs to the *T. laricis* Walker species group (Huggert 1983, Johnson 1984); both are new host records. Parasitoid impact on the predator, pooled for the two species, averaged 17% in 1994 (Conti *et al.* 1997, Roversi *et al.* in preparation).

Orange groves in Sicily are attacked by the phytophagous mirid *Calocoris trivialis* (Costa), which causes apical deformation of shoots, leaf necrosis and drop of flower buds (Barbagallo 1970). This mirid also has one generation per year and overwinters in the egg stage, but the eggs are embedded in the soft dead and decaying wood of old pruning wounds. These eggs are attacked by *Aprostocetus miridivorus* (Domenichini) (Barbagallo 1969, 1970, Graham 1987), *Aprostocetus* new species near *miridivorus* (Hymenoptera: Eulophidae) (Conti *et al.* 1991, 1997) and *Telenomus lopicida* Silvestri (Hymenoptera: Scelionidae) (Barbagallo 1970, Conti *et al.* 1991, 1997). Total parasitoid impact averaged 57–70% in the different years and locations (Barbagallo 1969, 1970, Conti *et al.* 1991, 1997, Roversi *et al.* in preparation). *Aprostocetus miridivorus* and *T. lopicida* were also recorded from overwintering eggs of the mirid *Capsodes lineolatus*, deeply embedded inside incisions in herbaceous plants (Silvestri 1932, 1939, Graham 1987). However, it is unknown whether the same parasitoids shift between two alternative hosts or if they are two different

biotypes, with different habitat preferences.

Some aspects of these mirid—egg parasitoid associations on oak and orange groves are described in this paper by combining observations on host oviposition sites and parasitoid morphological adaptations, with the aim of defining oviposition strategies.

MATERIALS AND METHODS

Sampling Procedures

Oak groves.—Field research on egg parasitoids associated with *C. quadripunctatus* was carried out in five permanent sampling areas with mixed stands of *Quercus pubescens* Will. and *Q. cerris* L., ranging from 350 m to 700 m above sea level, in central Tuscany (central Italy). *Quercus pubescens* is included in the overstorey, as the masts are more palatable to livestock, while *Q. cerris* is part of the understorey and is used mainly for timber. In this landscape of gently rolling hills, oak stands normally alternate with vineyards and olive groves.

During the winters of 1994 and 1996, 36 branches, 1 m long, were collected in each sampling area (total 180 branches) and transferred to the laboratory. All dead buds were counted, collected and kept under a shelter at outdoor conditions. In spring, when nymphs and parasitoids had emerged, buds were dissected and examined under the stereomicroscope.

Orange groves.—Overwintering eggs of *C. trivialis*, embedded in the soft decayed wood of the pruning wounds, were collected on 9–10 January 1991 and 2–5 February 1992 in 6 orange, *Citrus sinensis* (L.), groves, the same both years, in 5 localities of the Provinces of Catania and Siracusa (Sicily, southern Italy).

Pruning wounds of different sizes and suitable for oviposition by *C. trivialis* were sampled randomly over the whole area of the groves. Twenty (20) to 62 samples per grove were collected in 1991 (total 224

samples), 30 per grove in 1992 (total 180 samples). The samples were then transferred to the laboratory and kept under controlled conditions ($25 \pm 1^\circ\text{C}$, 60%-95% RH; photoperiod L:D 14:10) in different kinds of screened containers (30×160 mm glass tubes, 140×25 mm Petri dishes, $185 \times 140 \times 290$ mm plastic food containers), depending on the size of the samples. All the material was examined under the stereomicroscope in summer, when emergence of nymphs and parasitoids was complete.

Host Oviposition Sites and Parasitoid Structures

For both species of *Calocoris*, eggs were classified in the following categories:—healthy (i.e., eclosed),—parasitized (i.e., containing the parasitoid or with the presence of an emergence hole),—dead due to other agents (predators or unknown). Egg length was measured under a stereomicroscope and the characteristics of healthy and parasitized eggs were described. In the case of *C. quadripunctatus*, the distribution of healthy and parasitized eggs in each cluster was mapped.

The position of the parasitoid piercing point on the host egg was recorded when visible under the stereoscopic or compound microscope. However, on eggs of *C. trivialis* such parasitoid punctures are often hidden by remains of wood that are glued to the chorion, due to a sticky secretion from the ovipositing female. In an attempt to dissolve this secretion, eggs were sonicated at room temperature for at least 15 minutes in different solvents (water, ethanol, acetone, chloroform), or soaked in boiling chloroform (61.2°C) in a beaker inside a water bath for 15 minutes.

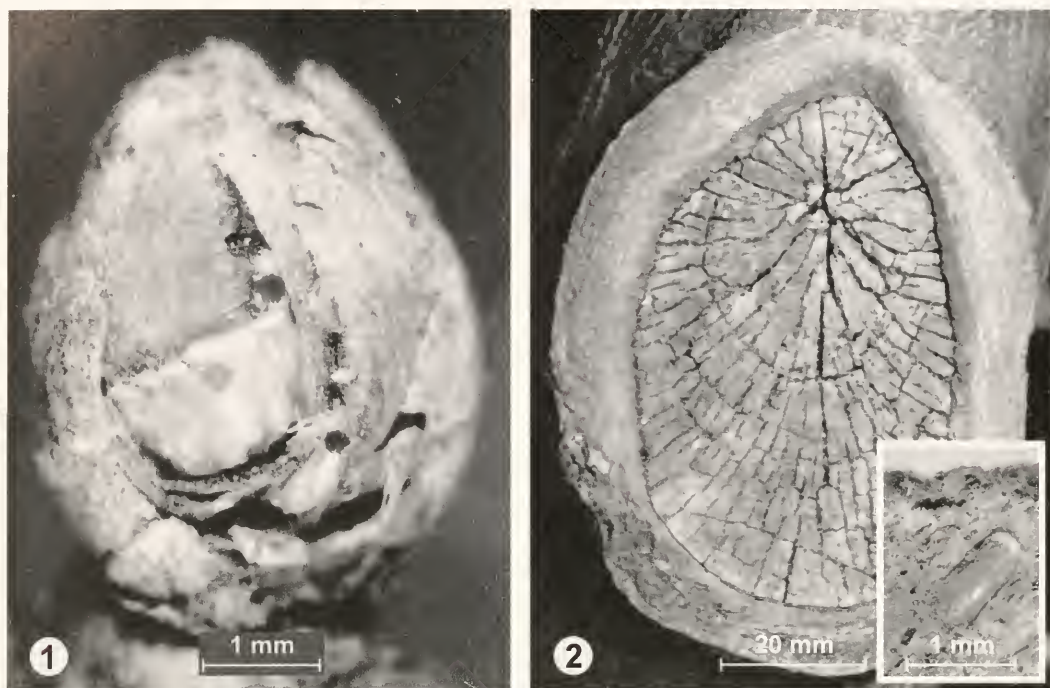
Parasitoids' structures used for reaching the concealed host eggs were evaluated by measuring the total body length, metasoma size and ovipositor length of 5 or 10 females of each species. To measure ovipositor length, the two scelionids were

cleared with potassium hydroxide and mounted on slides. Measurements were made using a micrometer eyepiece mounted on a compound microscope, or under a Nikon E 600 microscope connected to a JVC TK-C1380 video camera, and using a computer program for visual image analysis (Lucia 3.5).

RESULTS AND DISCUSSION

Host oviposition sites.—The eggs of *C. quadripunctatus*, concealed among the scales of dead buds on oak, are laid in clusters, most frequently with 3 to 5 eggs, and nothing appears externally to indicate their presence. In 1994 and 1996 buds with eggs contained on average 6 to 8 clusters each (Roversi *et al.* in preparation) (Figs. 1, 3 and 4). In contrast, the eggs of *C. trivialis*, concealed in the pruning wounds on orange trees, are laid singly and distributed variably on the wound surface where the decaying wood is soft enough for oviposition. The wounds sampled in 1991 and 1992 had a very variable diameter, from 13 to 98 mm, with an average of 45 mm. Wounds with eggs contained on average 8.3 eggs each in 1991 and 5.1 in 1992. Normally these eggs were deeply embedded, with the operculum at $386 \pm 37.2 \mu\text{m}$ (Mean \pm SEM, $n = 10$) under the substrate and not visible externally, although partially exposed eggs were also found in rare cases. The oviposition incisions, that indicate egg presence, may close partially or completely when rainwater swells the wood, thus becoming inconspicuous or totally invisible (Figs. 2, 11 and 12).

Both the dead buds on oak and the pruning wounds on orange trees contained recently laid eggs and eggs that had been laid during previous seasons, thus indicating that they provide a suitable oviposition substrate for several years. Also, because of wood erosion by atmospheric agents, old egg shells of *C. trivialis* on pruning wounds were often more or less exposed and directly visible



Figs. 1-2. 1, Dead oak bud partially dissected to show egg clusters of *Calocoris quadripunctatus* concealed between scales. 2, Pruning wound with soft decaying wood on orange tree and, in the inserted photo, a cross section partially exposing an embedded egg of *Calocoris trivialis*.

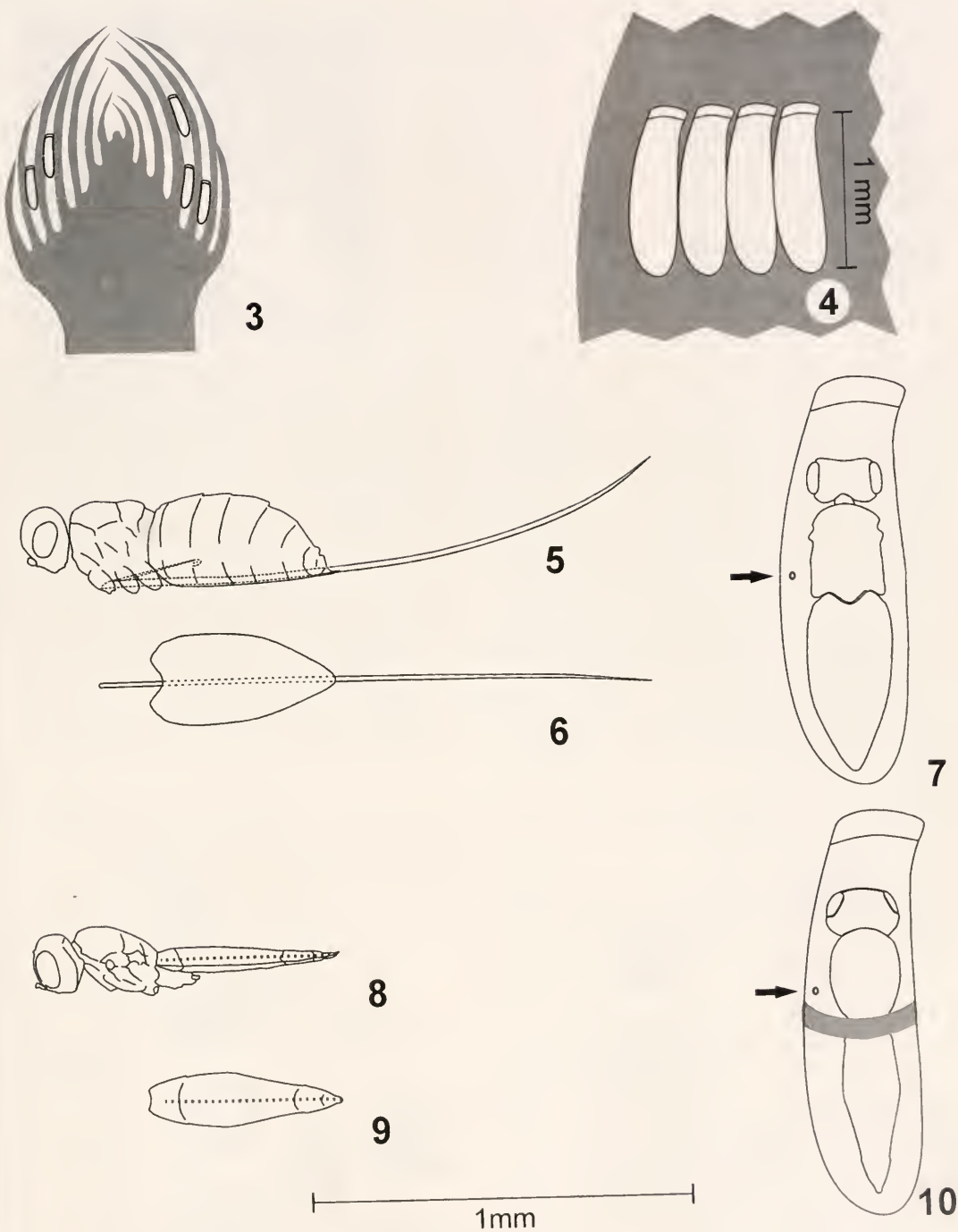
under the stereomicroscope or even to the naked eye.

Parasitoids' morphological adaptations and strategies.—How do the parasitoids reach and attack such concealed and, therefore, protected eggs?

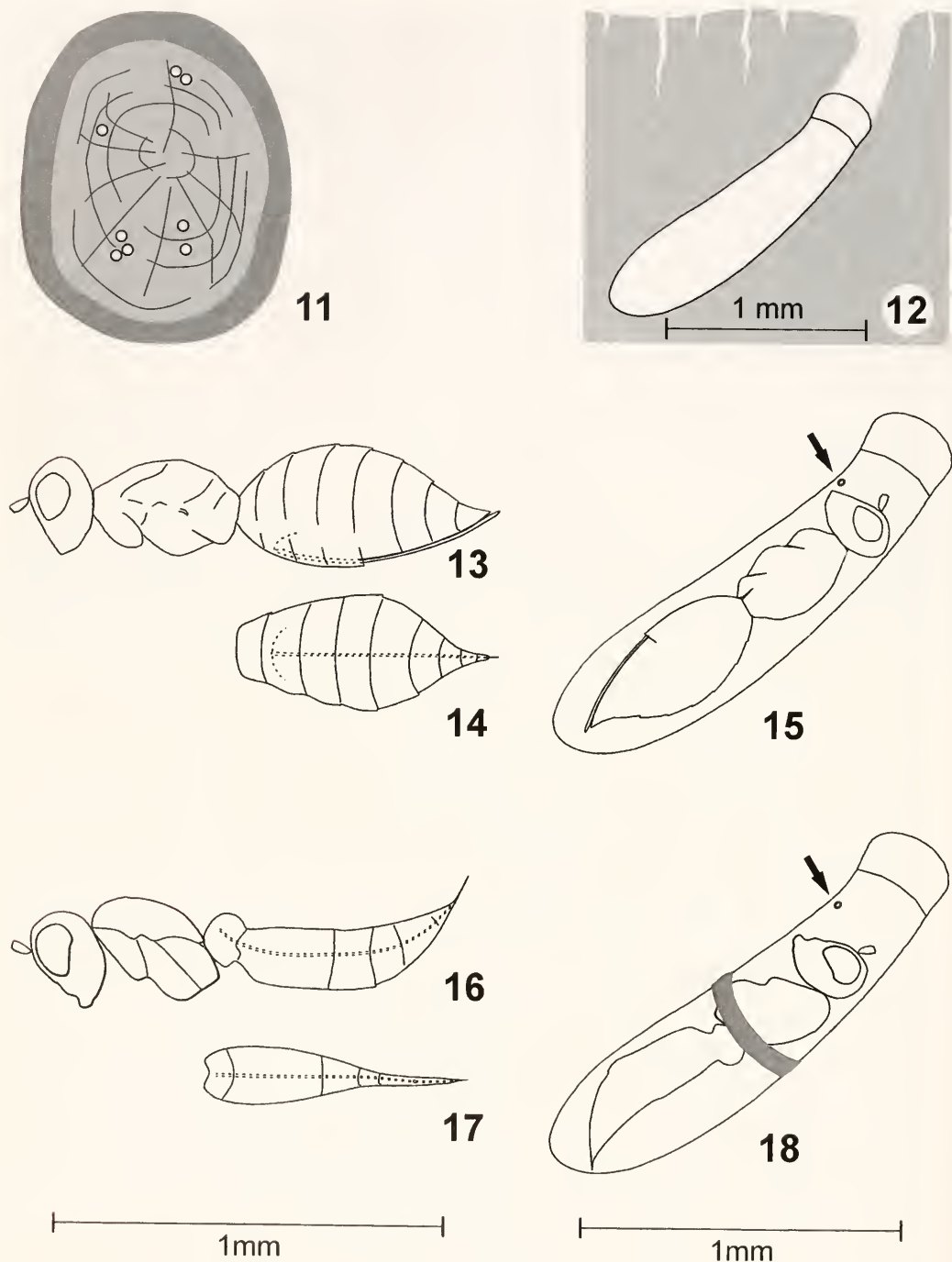
The egg parasitoids of *C. quadripunctatus* in oak buds have developed two different morphological adaptations and strategies (Figs. 5, 6, 8 and 9). The trichogrammatid *Chaetostricha walkeri* has a very long ovipositor, 3.15 times the length of its metasoma. The proximal end reaches the prothoracic coxae, where it is articulated on a special structure, probably used as an extension device (Figs. 5 and 6, Table 1). In contrast, the scelionid *Telenomus* sp. *laricis* group has a depressed (dorso-ventrally flattened) metasoma, 69% of the length of the whole body, which facilitates its insertion between bud scales. The ovipositor is 86% of the length of the metasoma and is invaginated in it, from which it is ex-

tended for parasitization (Figs. 8 and 9; Table 1). Similarly, lygaeid egg parasitoids in *Telenomus* and *Eumicrosoma* also have depressed metasoma (A. Polaszek, pers. comm.).

In spite of these adaptations, both *C. walkeri* and *Telenomus* sp. *laricis* group can hardly reach the most internal eggs, as only the first (peripheral) and second (sub-peripheral) ones are normally attacked, although there are a few exceptions (Roversi *et al.* in preparation). In addition, both parasitoids attack the peripheral egg more frequently than the sub-peripheral one, although *C. walkeri* can reach both much more often than *Telenomus* sp. (Fig. 19). Whether in such cases one species can discriminate between healthy eggs and eggs parasitized by the conspecific or other species is unknown. Similar differences of effectiveness, due to metasoma morphology and ovipositor length, were also observed on species attacking egg masses of the rice



Figs. 3–10. *Calocoris quadripunctatus* and its egg parasitoids. 3, Schematic section of a dead oak bud showing *C. quadripunctatus* egg clusters concealed between scales. 4, Detail of a scale with a cluster of four eggs. 5 and 6, Lateral and dorsal views of *Chaetostricha walkeri* Förster showing the long ovipositor. 7, Host egg parasitized by *C. walkeri* showing the parasitoid piercing point on the chorion. 8 and 9, Lateral and dorsal views of *Telenomus* sp. *laricis* group showing its depressed metasoma with the ovipositor indicated (dotted line). 10, Host egg parasitized by *Telenomus* sp. *laricis* group showing the parasitoid piercing point on the chorion and the characteristic transversal band.



Figs. 11-18. *Calocoris trivialis* and its egg parasitoids. 11, Example of a pruning wound on orange showing a distribution of *C. trivialis* eggs (circles). 12, Schematic section of a host oviposition incision to indicate egg position in relation to the substrate. 13 and 14, Lateral and dorsal views of *Aprostocetus* n. sp. near *miridivorus*. 15, Host egg parasitized by *Aprostocetus* n. sp. near *miridivorus* showing the parasitoid piercing point on the chorion. 16 and 17, Lateral and dorsal views of *Telenomus lopicida* showing its compressed metasoma with the long ovipositor indicated (dotted lines). 18, Host egg parasitized by *T. lopicida* showing the parasitoid piercing point on the chorion and the characteristic transversal band.

Table 1. Measurements (mean \pm SEM; in mm) of female parasitoid body parts to show morphological adaptations for reaching the host egg concealed between dead bud scales (*C. quadripunctatus*) or in decaying wood (*C. trivialis*).

Parasitoid	Host	Body length	Metasoma dimensions				
			Length	Lateral		Dorso-ventral (max.)	Ovipositor length
				Max.	Min.		
<i>Chaetostricha walkeri</i> ⁽¹⁾	<i>C. 4-punctatus</i>	0.843 \pm 0.022	0.479 \pm 0.015	0.268 \pm 0.005	—	0.274 \pm 0.010	1.511 \pm 0.029
<i>Telenomus</i> sp. ⁽²⁾	<i>C. 4-punctatus</i>	0.796 \pm 0.020	0.548 \pm 0.010	0.141 \pm 0.002	—	0.053 \pm 0.002	0.472 \pm 0.004
<i>Aprostocetus</i> sp. ⁽²⁾	<i>C. trivialis</i>	1.230 \pm 0.053	0.652 \pm 0.017	0.284 \pm 0.008	—	0.330 \pm 0.014	0.617 \pm 0.025
<i>Telenomus lopicida</i> ⁽²⁾	<i>C. trivialis</i>	1.095 \pm 0.018	0.635 \pm 0.015	0.162 \pm 0.004	0.027 \pm 0.005	0.146 \pm 0.007	0.832 \pm 0.039

⁽¹⁾ n = 10; ⁽²⁾ n = 5.

stemborer *Scirpophaga incertulas* (Walker) (as *Tryporyza incertulas* Walker) (Lepidoptera: Pyralidae) in Vietnam (Vu and Nguyen 1987) and on *Telenomus busseolae* Gahan attacking the maize stemborer *Sesamia nonagrioides* (Lefevre) (Lepidoptera: Noctuidae) in Greece (Alexandri and Tsitsipis 1990).

The egg parasitoids of *Calocoris trivialis* on orange have also developed two different strategies (Figs. 13, 14, 16 and 17). The eulophid *Aprostocetus* n. sp. near *miridivorus* shows no apparent morphological adaptations. The ovipositor is 95% of the

length of the metasoma and is probably introduced into the incision or inserted by drilling through the wooden substrate (Figs. 13 and 14; Table 1). Laboratory observations on the oviposition behavior of *A. miridivorus* towards *Calocoris norvegicus* (Gmelin), indicate that the parasitoid intensely antennates oviposition incisions containing host eggs and, in most cases, inserts its ovipositor through the incision, although it also appears to drill through the dead wood (Conti and Bin unpublished). This is especially important in the open field where, because of wood swell-

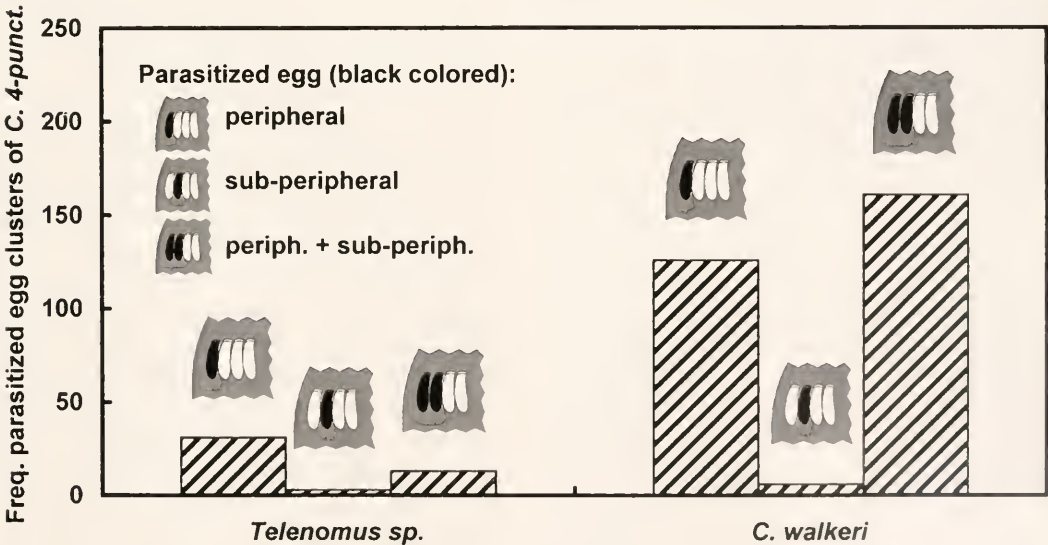


Fig. 19. Frequency of *Calocoris quadripunctatus* egg clusters (4 eggs per cluster on average) parasitized by *Telenomus* sp. *laricis* group or *Chaetostricha walkeri*, related to the position of the parasitized egg/s in the cluster. For the sake of clarity, the very few cases of more than 2 parasitized eggs per cluster have not been represented in the graph.

ing caused by rain, the incisions can be partially or completely closed.

The scelionid *T. lopicida* presents a much more evident adaptation. The distal half (53% of total length) of its metasoma is laterally compressed and its distal quarter (23%) is only 27 μm wide (Figs. 16 and 17; Table 1). This strongly facilitates its introduction into the host oviposition incisions, as has been observed with eggs of *Capsodes lineolatus* (Brullé) (Heteroptera: Miridae) embedded in stems of *Scabiosa columbaria* L. (Silvestri 1932, 1939). In addition, the ovipositor of *T. lopicida* is 1.31 times the length of the metasoma and is partially contained in a dorso-metosomal hump (Figs. 16 and 17; Table 1).

The parasitoid strategies described above are also confirmed by the position of the parasitoid piercing point on the egg chorion (Figs. 7, 10, 15 and 18). In the case of *C. quadripunctatus*, this point is evidenced by the presence of a brown circular area localized on the exposed side of the egg (Figs. 7 and 10). Such eggs, when parasitized by *C. walkeri*, are visibly swollen and light amber colored. In contrast, those attacked by *Telenomus* sp. *laricis* group are slightly opaque, with a dark transverse band evident from the pupal stage of the parasitoid onwards, and appear darker close to eclosion, due to the presence of the pupa or the adult, visible within.

In the case of *C. trivialis*, the parasitoid piercing point is less recognizable under the microscope because the darkened area is often not appreciable and because part of the chorion is generally hidden by wood remains glued to it. These remains could be removed only mechanically, when possible at all, as the glue is not soluble in any of the solvents tested. The piercing points, when distinguishable, were localized on the apical third of the concave egg side, under the egg cap area (Figs. 15 and 18). No piercing points on the egg cap were observed and, indeed, due to its thickness and hardness, it seems

that this area can be excluded as a piercing site by the parasitoid. Such parasitized eggs of *C. trivialis* were also characterized by a light amber-colored chorion and appeared darker close to eclosion because of the presence of the darkening pupa or the adult, visible within. Similar to *C. quadripunctatus*, eggs of *C. trivialis* parasitized by *T. lopicida* show a dark transverse band at the level of the metathorax (Fig. 18) while those parasitized by *Aprostocetus* sp. do not show any particular pattern (Barbagallo 1969, Mineo and Sinacori 1978) (Fig. 15).

Escaping from the host substrate is another critical situation for which the emerging parasitoids, both males and females, need a morphological adaptation (Quicke 1997). Parasitoids of *C. quadripunctatus* in most cases escape from the buds by crawling out between the scales, although *C. walkeri* may also chew circular holes in the scales. In contrast, both parasitoids of *C. trivialis* have to chew a hole of variable length in the soft decaying wood, depending on their distance from the surface. While in most cases the emergence hole of both species is localized in the apical third of the egg, including the egg cap area, sometimes *T. lopicida* pupates upside-down and therefore has to chew a much longer tunnel in the wood. This is obviously performed with mandibles well adapted to chew plant tissues.

No other adaptive cephalic feature is presented by *T. lopicida* since its frons is smooth, whereas other species, also belonging to the *T. laricis* group, exhibit a marked scale-like sculpture on the frons and vertex (Johnson 1984) probably useful for escaping in combination with mandibles (Bin and Conti unpublished) and have a pointed head, the distinctive feature of the *laricis* group (A. Polaszek, pers. comm.).

CONCLUSIONS

Ideally, host-parasitoid associations should be defined using a complete set of

characters, ranging from physical and chemical cues for habitat and host location, to physiological and biochemical interactions for host suitability. However, some pieces of such a complex mosaic can be provided by comparing the features of the microhabitat, selected by the host to escape adverse climatic events, with the ability of the parasitoid to overcome such physical barriers in order to reach the host and eventually emerge from it.

It is clear that in some cases the morphology of the ovipositor (Austin 1983), the metasoma and, possibly, other body parts are evolutionarily linked to the exploitation of particular hosts. Therefore, in the future these morphological adaptations may be used to predict the most likely host groups or oviposition sites (Austin 1983).

The parasitoid species considered here appear to be well adapted for reaching their concealed host eggs, and the morphological adaptations especially involve the metasoma and/or the ovipositor system. Their oviposition strategies can be defined by comparison with similar strategies described in the literature (Gauld and Hanson 1995, Smith *et al.* 1993; Smith and Wiedenmann 1997), although more direct observations are needed to better understand their behavior. *Chaetostricha walkeri* inserts its long ovipositor between bud scales and is therefore an "ovipositor prober". *Aprostocetus* n. sp. near *miridivorus* is both an "ovipositor prober" and an "ovipositor driller", as it probably inserts its terebra either inside the host oviposition wound or through the soft wooden substrate. In contrast, both *Telenomus* species are "metasomal probers". In fact, their metasoma is adapted to reach the host eggs by inserting at least part of it into the host oviposition sites, specifically between bud scales in the case of *Telenomus* sp. *laricis* group, or in the host oviposition incision in the case of *T. lopicida*.

We have shown that *Chaetostricha walkeri* is an egg parasitoid of *Calocoris quad-*

ripunctatus. This is a new host record and it suggests that previous ones were erroneous. In fact, *C. walkeri* has been reported from eggs of *Tortrix viridana* (Kolubajiv 1959 according to Du Merle 1983, Martinek 1963), from the coccid *Leucaspis pinii* Htg. (Nikol'skaya 1952), or from unknown hosts, supposedly xylophagous larvae (Silvestri 1917 citing Föster) or Heteroptera eggs embedded in wood (Silvestri 1917). The eggs of *C. quadripunctatus*, the true host, were evidently overlooked because they were not visible externally.

Many of the available host records for other *Telenomus* species in the *laricis* group are similarly questionable, and a careful reassessment is needed before supposed host associations can be accepted as reliable.

ACKNOWLEDGMENTS

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New Caledonian Tiphiiidae: Revision of the Genus *Eirone* (Hymenoptera: Thynninae)

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Abstract.—Ten new species of New Caledonian *Eirone* are described based on males, including *anone* Kimsey, *irwini* Baptiste, *koghisica* Kimsey, *laniensis* Baptiste, *maigretae* Baptiste, *nasalis* Kimsey, *nepouiensis* Baptiste, *paniensis* Kimsey, *rivierensis* Baptiste, and *webbi* Kimsey. In addition, females of *irwini*, *transversa* Brown, *nepouiensis*, and *webbi*, are also described. Male genitalia are described and illustrated for both the new species and for the first time for *colorata* Brown, *marginata* Brown, *neocaledonica* Turner, *nigra* Brown, *obtusidens* Turner, *salteri* Brown, *subtuberculata* Brown and *transversa* Brown. These previously described species are also rediagnosed. A key to males of the species of New Caledonian *Eirone* is also included.

As recently as the early 1980's only nine species of *Eirone* Westwood were known from New Caledonia (Brown 1984). Subsequent malaise trap collecting by Michael Irwin, Evert and Marion Schlinger and Donald Webb have demonstrated that the thynnine fauna of New Caledonia is substantially richer than previously thought. Their efforts have turned up ten undescribed species of *Eirone*. Based on their collecting efforts, *Eirone* appears to be the only thynnine genus present on New Caledonia.

MATERIALS AND METHODS

Specimens were obtained for this study from the following institutions and individuals: Bernice P. Bishop Museum, Honolulu, Hawaii, G. Nishida (HONOLULU); Illinois Natural History Survey, University of Illinois, Champaign-Urbana, M. E. Irwin (URBANA), Canadian National Insect Collection, Ottawa, Ontario, L. Masner (OTTAWA), University of California, Davis, S. L. Heydon (DAVIS). Holotypes of the new species described below will all be deposited in the Muséum Nationale d'Histoire Naturelle, Paris (PARIS). The type of *Eirone impunctata* Brown was to

have been deposited in the collection of the Rydalmere Quarantine Station, NSW. This collection has been moved to the Agricultural Scientific Collections Unit, NSW Agriculture, Orange Agricultural Institute, Orange, Australia (P. S. Gillespie). However, the type cannot be located. Specimen and type repositories are indicated in the text by the city name in capital letters.

The following abbreviations are used for the sake of brevity: F = flagellomere, MOD = midocellus diameter, PD = puncture diameter.

SPECIES DESCRIPTIONS

Eirone anone Kimsey, new species (Fig. 19)

Male.—Body length 15–18 mm; forewing length 12–14 mm; face with tiny contiguous punctures between inner eye margins and antennal sockets; frons with punctures 0.5–2 apart, except impunctate along medial sulcus and adjacent to antennal socket; clypeus with punctures larger than along inner eye margin, punctures contiguous; clypeal apex broadly triangular, with single apicomedial lobe; F-I length 2.4–2.5× breadth; F-II length 3.0–

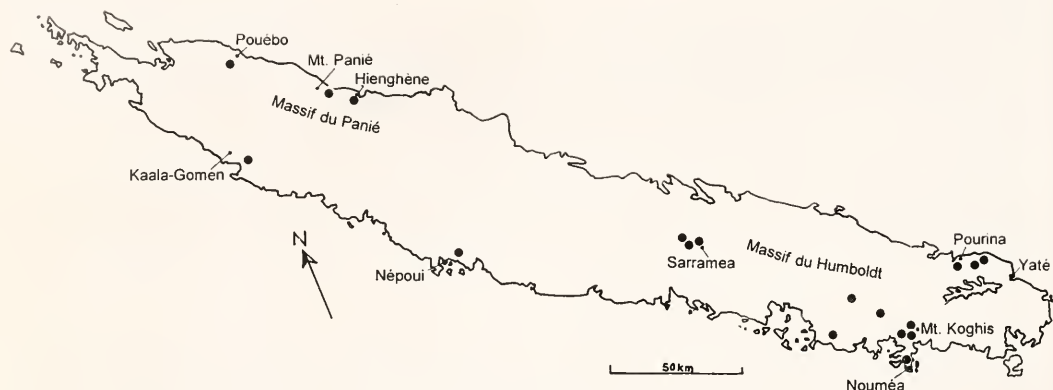


Fig. 1. Distribution map of *Eirone* species in New Caledonia.

3.2× breadth; pronotal punctures 1–3 PD apart; mesopleural punctures 1–2 PD apart separated by dense, fine shagreening; mesopleural lamella posteriorly rounded; scutal punctures densest along notauli (nearly contiguous), medially sparsest (0.5–1 PD apart); scutellum nearly impunctate medially, punctures denser laterally, 0.5–1.0 PD apart; propodeum punctate medially and laterally, punctures 0.5–1.0 PD apart, impunctate sublaterally; metasomal sternum I sharply keeled and somewhat hooked posteriorly, abruptly declivous posteriorly; epipygium and hypopygium flattened and apex narrowly subtruncate; genital capsule (Fig. 19): gonocoxa with medial angular lobe on inner surface; aedeagus apical column broad, and flattened apically, ending abruptly with rounded basal angle and narrow, hooked apical lobe, column extending more than half its length beyond penis valve bending dorsally; penis valve with short dorsal hook, hooked ventral lobe and elongate basal lobe; volsella with hooked bilobate dorsal surface and obsolescent asetose ventral surface; color: orange, with extensive black markings on vertex, extending down along side antennal sockets, on occiput, pronotum anteriorly and medially, scutum except large yellow medial spot, mesopleural margins, scutellum anteromedially, coxae dorsally, propodeum anterior margin black to en-

tirely black, metasomal segments I and VI entirely black, segment VII anterior margin black; gonocoxa orange; wing membrane yellow-tinted, veins black; vestiture long, erect and orange-colored.

Type material.—Holotype ♂; trail to Mt. Panié, 22 km NW Hienghène, 11–25 Nov. 1992, Webb & Schlinger, malaise trap (PARIS). Paratypes: 15 ♂♂, same data as holotype; 3 ♂♂, Mt. Mandjanié, 5.3 km WSW Pouébo, 500 m, 9–26 Nov. 1992, D. W. Webb, malaise trap (DAVIS, ILLINOIS). This species was collected in November.

Etymology.—The species name, *anone*, is a nonsense combination of letters, assumed to be feminine.

Discussion.—This species closely resembles *obtusidens* in coloration, presence of a midcoxal spine, rounded mesopleural lamella, and unilobate, densely setose clypeus. It can be immediately separated from *obtusidens* by the strongly keeled metasomal tergum I and apically acute aedeagus. The unilobate clypeus is unique to these two species.

Eirone colorata Brown

(Fig. 9, 22)

Eirone colorata Brown 1984:254. Holotype ♂: New Caledonia: Col de Ho (HONOLULU), examined.

Male.—Body length 12–15 mm; fore-

wing length 9–12 mm; face with tiny contiguous punctures between inner eye margins and antennal sockets; frons with punctures 1–4 PD apart; clypeus with punctures larger than along inner eye margin, punctures 0.5–1.0 PD apart; clypeal apex broadly truncate, 2.6–2.8 MOD wide; F-I length $2.2\times$ breadth; F-II length $2.8\times$ breadth; pronotal punctures 1–4 PD apart; mesopleural punctures 1–2 PD apart, finely, shagreened between; mesopleural lamella rounded apically; scutum medially, with punctures 1.0–1.5 PD apart, punctures becoming finer and denser laterally, 0.5–1.0 PD apart; scutellar punctures 1–4 PD apart; propodeum punctate medially and laterally, punctures 0.5–1.0 PD apart, impunctate sublaterally, finely and densely shagreened between punctures; midcoxa with apical spine (Fig. 9); metasomal sternum I keeled medially, keel extending two-thirds of length, sloping obliquely to posterior margin; epipygium and hypopygium flattened and broadly rounded apically; genital capsule (Fig. 22): gonocoxa with low submedial angular projection on inner surface; aedeagus unmodified, with slender apical column extending less than half its length beyond penis valve, and bending ventrally; penis valve saddle-shaped with short dorsal hook; volsella with small bilobate dorsal projection and ventral surface with 6–8 long erect setae; color orange, becoming yellower on face, pronotum, tegula and subalar region of mesopleuron; scape orange, flagellum dark brown, black markings on vertex, pronotal middle, scutum black except large medial mark and sides yellow, scutellum anteriorly black, propodeum anteriorly, mesopleuron along dorsal margin, coxae and femoral dorsal margin, metathorax laterally, apical abdominal segments darker; wing membrane yellow-tinted, veins black; pubescence silvery on head and thorax and black on metasoma.

Material examined.—21 ♂♂ (including the holotype); Col de Ho, 22 km NW

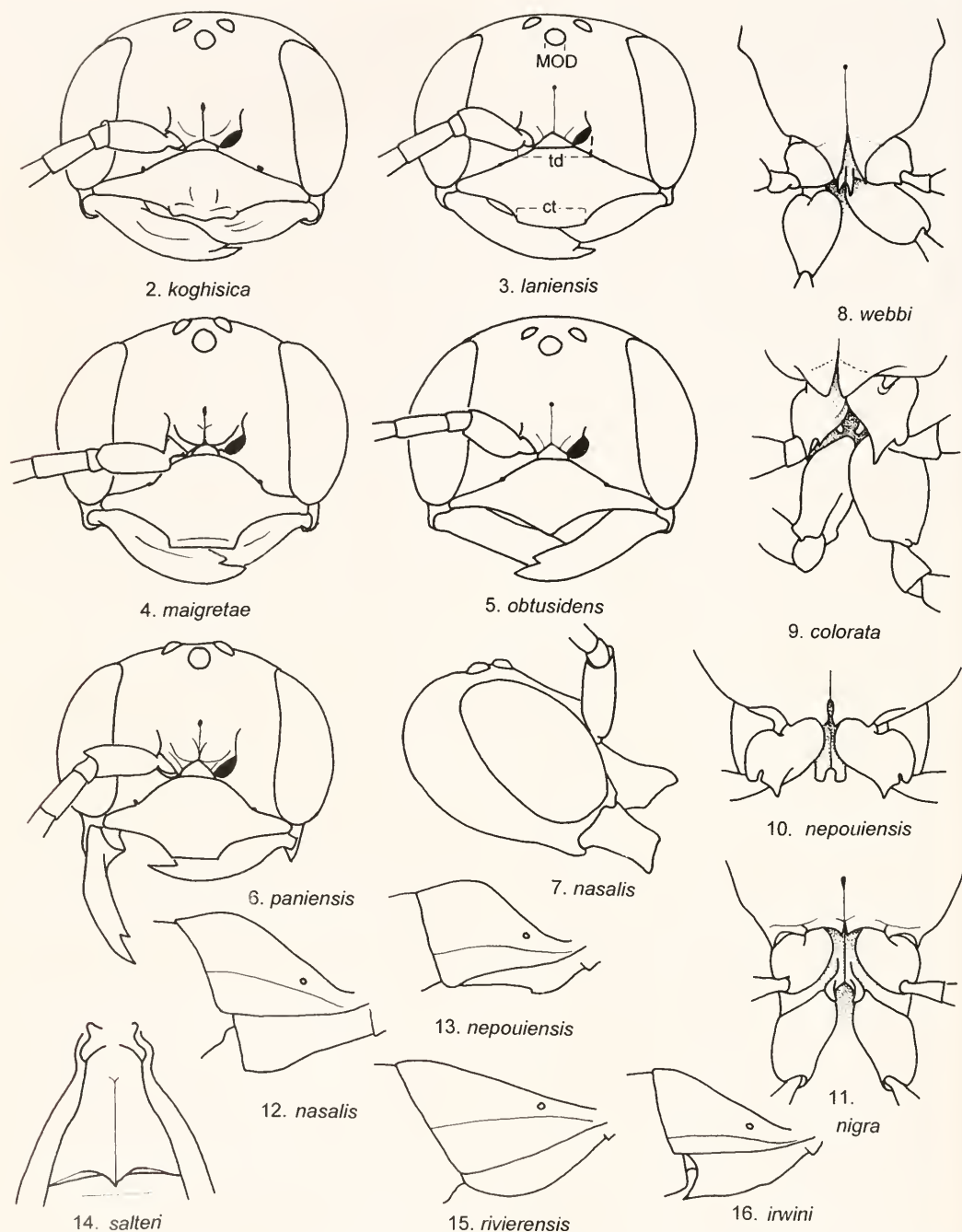
Hienghène (trail to Mt. Panié), and Mt. Panié, 9.7 km NW Sarraméa. These specimens were collected in the months of October, November, January and February.

Discussion.—*Eirone colorata* most closely resembles *rivierensis* based on the emarginate mesopleural lamellae, midcoxal spine, metasomal sternum I obliquely sloping posteriorly, and apically truncate clypeus. The two species differ in the vestiture of the abdominal terga, *rivierensis* has dense tufts of long black setae on T-VI and VII, which are lacking in *colorata*, and the aedeagus of *colorata* is small and unremarkable, whereas the apical aedeagal column in *rivierensis* is broadly flattened and subtriangular. Finally, *colorata* specimens are at least partly reddish orange, whereas *rivierensis* specimens lack this reddish orange coloration.

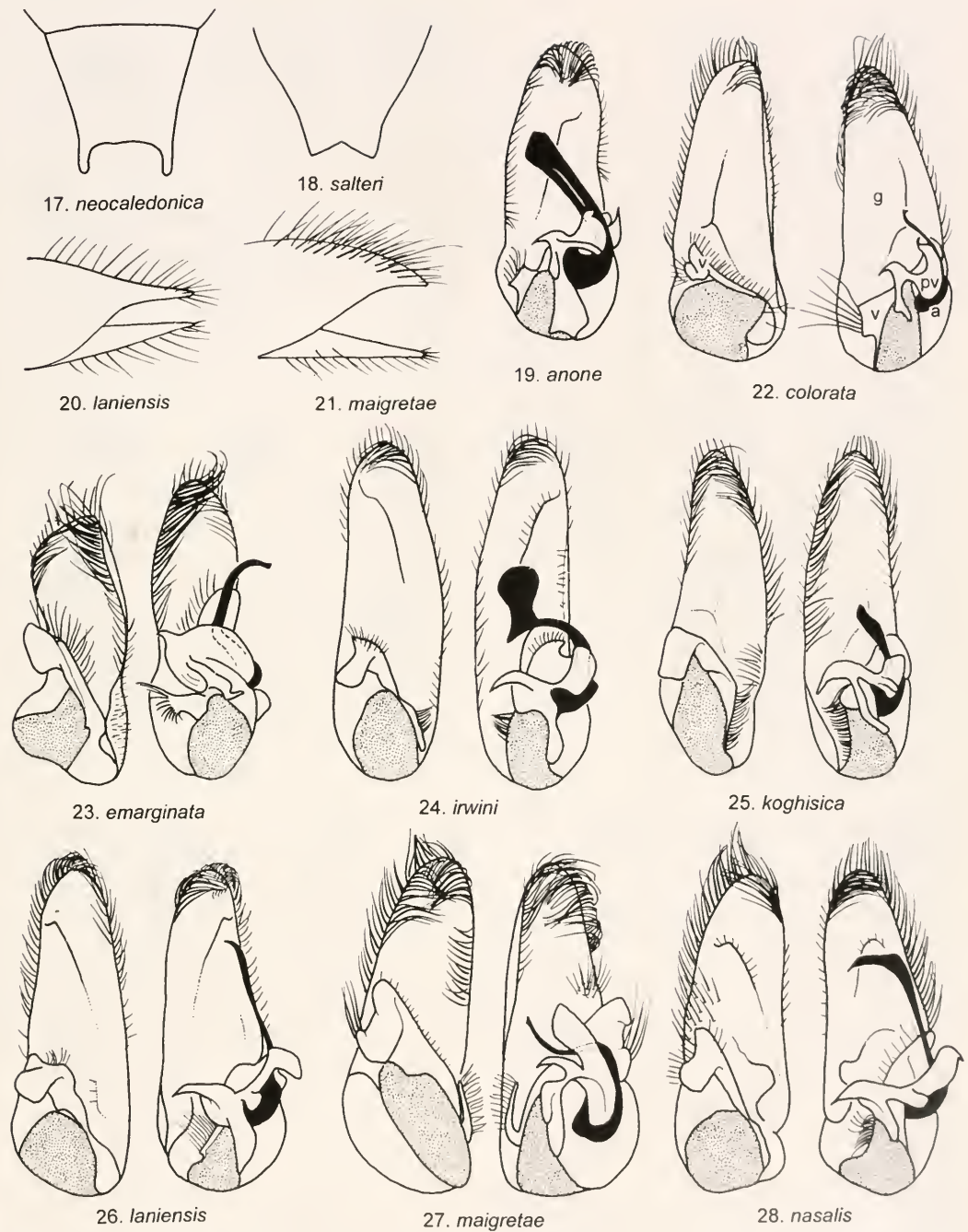
Eirone emarginata Brown (Fig. 23)

Eirone emarginata Brown 1984:256. Holotype ♂; New Caledonia: Col des Rousettes (HONOLULU), examined.

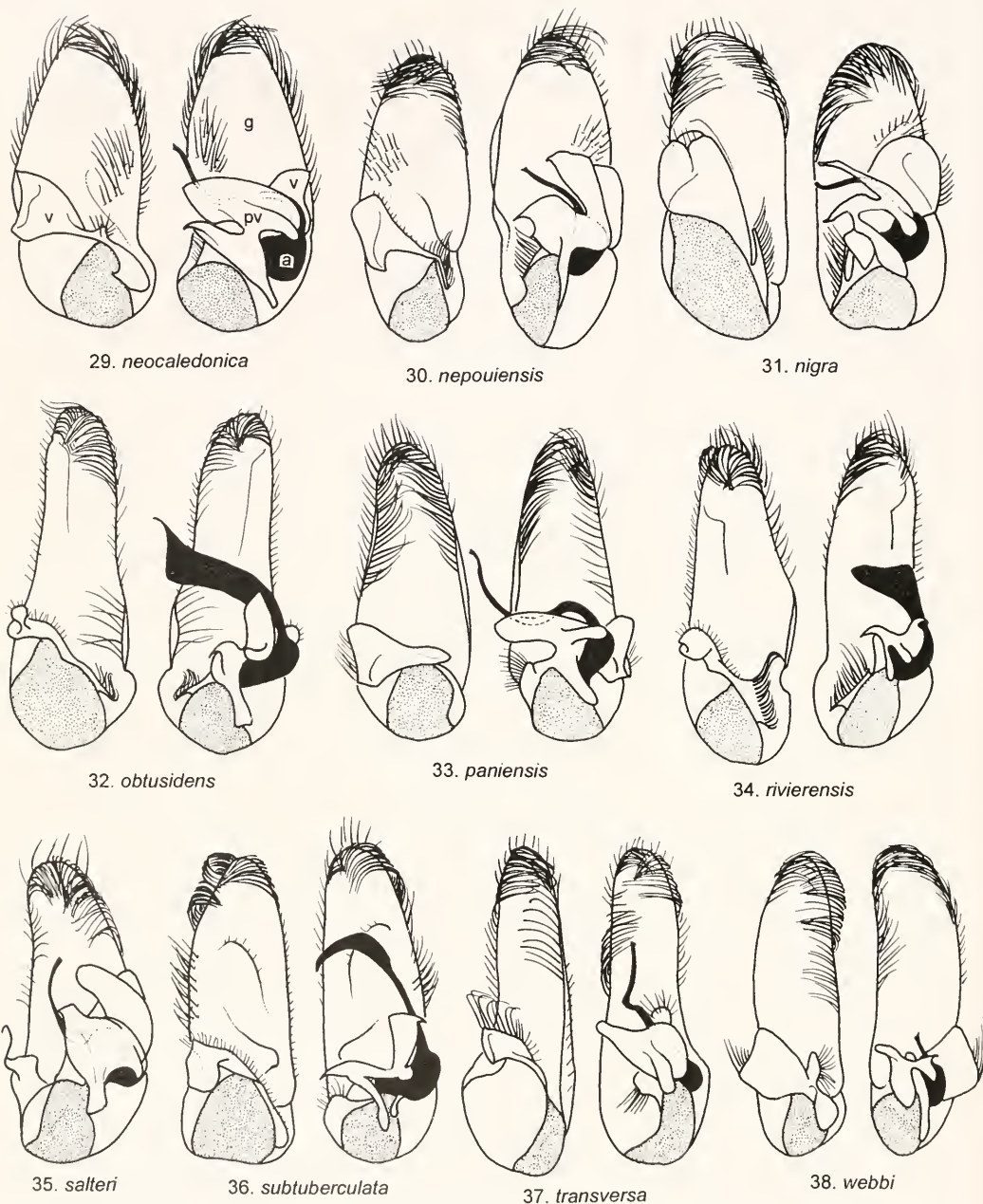
Male.—Body length 16–21 mm; forewing length 11–15 mm; face with tiny, contiguous punctures between inner eye margins and antennal sockets; frons with punctures irregular, 0.5–1.0 PD apart, except impunctate medial sulcus; clypeus convex medially, with punctures larger than along inner eye margin, punctures contiguous to 0.5 PD; antennal lobe with small subsidiary ventrally projecting lobe; clypeal apex medially emarginate, acutely pointed on either side, 2.6 MOD wide; F-I length $2.5\times$ breadth; F-II length $3.0\times$ breadth; pronotal punctures 0.5–1.0 PD apart; mesopleural punctures 0.5 PD apart; mesopleural lamella short, posteriorly emarginate; scutal punctures medially 0.5–1.0 PD apart, becoming finer and nearly contiguous laterally; scutellar punctures large and 0.5–1.0 PD apart near midline becoming smaller, denser and nearly contiguous laterally; propodeum



Figs. 2-16. *Eirone* species. 2-6, Front view of male face, with right antenna removed. 7, Lateral view of male face. 8, 10, Ventral view of male meso- and metathorax. 9, Oblique ventral view of male meso- and metathorax. 11, Ventral view of male mesothorax. 12-15, Lateral view of male metasomal segment I. 16, Ventral view of male metasomal segment I. Abbreviations: ct = clypeal truncation, MOD = midocellus diameter, td = transantennal distance.



Figs. 17–28. *Eirone* species. 17–19, Dorsal view of male epipygium. 20–21, Lateral view of male abdominal apex. 22–28, Interior surfaces of genital capsule. Abbreviations: a = aedeagus, g = gonocoxa, pv = penis valve, v = volsella.



Figs. 29–38. *Eirone* species, Interior surfaces of genital capsule. Left side gonocoxa and volsella. Right side penis valve uppermost. Inner margins of both sides are the ventral surface of the genital capsule; outer margins are the dorsal surface. 35, Right side of genital capsule only. Abbreviations: a = aedeagus, g = gonocoxa, pv = penis valve, v = volsella.

punctate medially and laterally, punctures 1–2 PD apart, impunctate sublaterally; midcoxa without apical spine; metasomal sternum I with short, carinate medial keel

extending half length, sloping obliquely to posterior margin; epipygium strongly convex, posterior margin broadly rounded, with slight indentation medially; hypo-

pygium flat, broadly rounded apically; thorax and metasoma finely and densely shagreened between punctures; genital capsule (Fig. 23): gonocoxa narrowed medially, inner surface smooth without projections, ridges or lobes; aedeagus apical column elongate, extending more than half its length beyond penis valve, bending abruptly ventrally; penis valve leaf-like with small dorsal hook; volsella with large hoof-like dorsal lobe, ventral lobe with short spine-like setae; color black, with small, pale yellow spot on antennal lobe, genital capsule yellow to orange; wing membrane brown-tinted, veins black; pubescence silvery.

Material examined.—9 ♂♂ (including the holotype); 22 km NW Hienghène; Rivière Bleue Prov. Pk., km 25.8 Rivière Bleue Road; 7.5 km NW Sarraméa; 17 km nne Nouméa; Rivière Bleue Prov. Pk., trail to Valle de Pourina (DAVIS, HONOLULU, URBANA). Specimens were collected in October, November and February.

Discussion.—As discussed under *webbi*, there are five species of New Caledonian *Eirone* that lack a midcoxal spine. Of these *emarginata* and *maigretae* are most similar. Both are large-bodied, with the epipygium broadly rounded apically and strongly convex in profile, and both have a sharply cornered clypeal truncation. Diagnostic features of *emarginata* include the medially emarginate clypeal truncation, black body and apically truncate hypopygium.

Eirone impunctata Brown

Eirone impunctata Brown 1984:256. Holotype ♂: New Caledonia: Forêt de la Thy (Repository?).

Material examined.—No specimens of this species have been seen. The type is apparently unavailable. According to Brown (1984) the holotype was collected in April.

Discussion.—See *webbi*.

Eirone irwini Baptiste, new species (Figs. 16, 24)

Male.—Body length 15–17 mm; forewing length 12–14 mm; face with small, nearly contiguous punctures between inner eye margins and antennal sockets; frons with punctures 0.5–1 PD apart, except nearly impunctate medial longitudinal band; clypeus with punctures much larger than along inner eye margin and nearly contiguous; clypeal apex weakly trilobate, with medial lobe extending furthest, distance between outer lobes 3.3 MOD; F-I length $2.4\text{--}2.5\times$ breadth; F-II length $3.4\text{--}3.5\times$ breadth; pronotal punctures 1–3 PD apart; mesopleural punctures 1–2 PD apart medially, finely shagreened between; mesopleural lamella apically rounded and bending slightly ventrally; scutal punctures medially 1–2 PD apart, becoming finer and denser laterally 0.5 PD apart; scutellar punctures 1–1.5 PD apart, except for medial longitudinal impunctate stripe; propodeum punctate medially and laterally (punctures 1–2 PD apart), impunctate along sublateral band and above petiolar socket; metasomal sternum I sharply keeled medially, sloping obliquely to pointed apex, apex extending over base of metasomal sternum II (Fig. 16); epipygium narrowed and flattened apically, apical margin indented medially; hypopygium narrowly rounded apically; genital capsule (Fig. 24): gonocoxa with protruding submedial longitudinal ridge; aedeagus apical column arcuate, with apical flag, strongly bending dorsally; penis valve saddle-shaped, with long dorsal hook; volsella with large bilobate dorsal end, ventral part short, with brush of dense, stout setae. Body black, with yellow or cream-colored markings on: lower half of inner eye margins, lower two-thirds of outer eye margins, spot on upper inner of eye margin, spot on antennal lobe, transverse band on anterior carina of pronotum, anterolateral spot on pronotum, tegula basally, anterolateral edge of

scutellum, submedial spots on metanotum; wing membrane light brown, darkest near apex, with black veins; vestiture black on face and metasoma, silvery on rest of head and thorax.

Female.—Body length 11 mm; head and thorax coarsely punctate, punctures contiguous to 0.5 PD apart; abdominal punctures slightly smaller and 0.5–1.0 PD apart; frons with medial longitudinal sulcus, extending more than halfway to posterior head margin; clypeal margin centrally concave and pointed apically; F-I length $1.3\times$ breadth, F-II length $1.6\times$ breadth; propodeum subrectangular in dorsal view, with transverse basal carina and lateral edge marked by sharp carina; T-I punctures longitudinally striatiform; metasomal sternum I with short medial longitudinal carina; body dark brown to black, with pale, silvery setae.

Type material.—Holotype ♂ (flagellomeres affixed to point below specimen): NEW CALEDONIA, Sarraméa, 24 Dec. 1991, M. E. Irwin (PARIS). Paratypes: 6 ♂♂, 3 ♂♂, same data as holotype; 1 ♂, 1 ♀ (in copula), Sarraméa, 24–25 Dec. 1991, M. E. Irwin, D. W. Webb, malaise trap across forest opening; 1 ♂, trail to Mt. Panié, 22 km NW Hienghène, 11 Nov. 1992, D. W. Webb, E. & M. Schlinger, malaise trap in tropical rainforest, 457 m (DAVIS, ILLINOIS). This species was collected in November and December.

Etymology.—The species is named in honor of the collector, Michael E. Irwin.

Discussion.—Males of both *irwini* and *nigra* share the oddly keeled metasomal sternum I, and both are black with pale markings. However, *irwini* can be immediately distinguished by the presence of a midcoxal spine and fully developed mesopleural lamellae. The shape of the aedeagus is also unique to *irwini*.

***Eirone koghisica* Kimsey, new species**
(Fig. 2, 25)

Male.—Body length 11–13 mm; forewing length 10–11 mm; face (Fig. 2), punctures widely separated on frons and vertex, 2–4 PD apart, becoming smaller and denser toward inner eye margin, tiny and contiguous between inner eye margin and antennal socket; clypeal punctures contiguous and somewhat striatiform medially; clypeal apex slightly flared anteriorly, slightly depressed medially when viewed in profile, apex weakly trilobate and 3 MOD wide between outer lobes; F-I length $2\times$ breadth; F-II length $2.3\times$ breadth; pronotal and scutal punctures sparse and 2–4 PD apart medially, becoming smaller and denser laterally, contiguous to 0.5 PD apart; mesopleural punctures 0.5–1.0 PD apart; scutellum impunctate basally, becoming punctate posterolaterally, punctures 0.5–1.0 PD apart; propodeum finely shagreened, punctures 0.5–1.0 PD apart, with impunctate sublateral area; midcoxal spine present; abdominal segments finely shagreened, with scattered punctures 2–4 PD apart; metasomal sternum I with medial keel extending three-fourths of total length, abruptly declivitous posteriorly; epipygium with narrowly rounded apex; hypopygium with narrowly rounded apex; genital capsule (Fig. 25): gonocoxa with submedial welt or swelling on inner surface; aedeagus apical column bending dorsally, with apex broadened; penis valve with large dorsal hook; volsella dorsally broadened and subrectangular, ventrally with brief row of dense short setae or spines. Body black, with pale yellow or cream-colored markings on lower three quarters of inner and outer eye margins, antennal lobes, transverse band on lower face from mandibular bases across clypeus, mandibular base, transverse band along anterior pronotal carina broken medially, arc on posterior lobe of pronotum near tegula, basally on tegula, scutum at posterolaterally, metanotum medially; wing membrane brown becoming darker in medial cell, with brown veins; vestiture silvery on head and thorax, black on metasoma.

Female.—Unknown.

Type material.—Holotype ♂: NEW CAL-EDONIA, Prov. Sud, Mt Koghis, 17 km nne Nouméa, malaise across path in rain-forest, 425m, 8–10 Jan. 1996, M. E. Irwin, D. W. Webb, E. I. Schlinger, 22°10'34"S 166°30'17"E (PARIS). Paratypes: 6 ♂♂, 2 ♂♂, Rivière Bleue Prov. Pk., trail to Upper Rivière Bleue, 19–28 Nov. 1992, 305 m, D. W. Webb; Rivière Bleue Prov. Pk., km 21.9 Rivière Bleue road, Nov. 1992, 290 m, M. E. Irwin, D. W. Webb; 2 ♂♂, same as previous, except, 5–16 Nov. 1992, 290 m, D. W. Webb; 1 ♂, Rivière Bleue Prov. Pk., trail to Vallée de Pourina, 19–28 Nov. 1992, 850 m, D. W. Webb; 1 ♂, Mt Koghis, 17 km nne Nouméa 5–15 Nov. 1992, D. W. Webb (DAVIS, ILLINOIS). This species was collected in November and early January.

Etymology.—This species is named after the collection site on Mt. Koghis.

Discussion.—*Eirone khogisica* most closely resembles *laniensis*, based on the apically convex clypeus, shallowly convex metasomal sternum I, presence of a midcoxal spine and well-developed mesopleural lamella. Both species are basically black with yellow to whitish markings. However, *koghisica* can be distinguished from *laniensis* by the trilobate clypeus, and apically rounded or truncate epipygium.

***Eirone laniensis* Baptiste, new species**
(Figs. 3, 20, 26)

Male.—Body length 10–16 mm; forewing length 9–13 mm; face (Fig. 3); punctation as in *koghisica*, except clypeal punctures 1–2 PD apart; clypeal apex gently convex medially and 2.5 MOD wide; F-I length 2.3× breadth; F-II length 3.6× breadth; midcoxal spine present; metasomal sternum I with medial longitudinal carina extending about halfway from anterior edge; epipygium with narrowly truncate bilobate apex, medially depressed subapically, with long setae arising from margins, strongly flattened in profile; hypopygium narrowly rounded apically and flattened in profile, with

short, stout fringe of setae along apex (Fig. 20); genital capsule (Fig. 26): gonocoxa with subapical ridge; aedeagus with apical column slender and elongate, extending two-thirds length of gonocoxa, bending dorsally; penis valve appearing strongly trilobate, with long dorsal hook; volsella strongly bilobate dorsally, ventrally with densely setose surface. Head black, with yellow or cream-colored markings on antennal lobes, lower half of clypeus, inner and outer eye margins, spot behind eye, base of mandible; pronotal band on anterior carina, on pronotal lobe near tegula; mesopleuron black, with yellow spot below tegula; scutum black with yellow spot basally on tegula; scutellum and metanotum with yellow markings medially and on anterolateral edge; propodeum with posterior yellow submedial spots; legs orange, except coxae black with yellow-orange ventral markings ventrally; metasoma orange, with black markings basally and apically on T-I, apically on metasomal sternum II and T-V, T-VI, metasomal sternum I, S-V and S-VI entirely black; wing membrane light brown with dark brown veins; vestiture silvery on head and thorax, orange on metasomal except black in specimens from Mt. Koghis and Mt. Dzumac.

Female.—Unknown.

Type material.—Holotype ♂: NEW CAL-EDONIA, Upper La Ni Valley, 2–17 Nov. 1992, D. W. Webb, 103 m, malaise trap across logging road (PARIS). Paratypes 42 ♂♂, 34 ♂♂, same data as holotype; 2 ♂♂, Rivière Bleue Prov. Pk., trail to Vallée de Pourina, 19–28 Nov. 1992, 850 m, D. W. Webb, malaise trap across forest path; 1 ♂, Rivière Bleue Prov. Pk., km 25.8, Rivière Bleue road, 30 Oct – 3 Nov. 1992, 213 m, M. E. Irwin, D. W. Webb; 2 ♂♂, Mt. Koghis, 500 m, 17 km nne Nouméa, 5–15 Nov. 1992, D. W. Webb; 1 ♂, Mt. Koghis, 500 m, 17 km nne Nouméa, 1–3 Nov. 1992, M. E. Irwin, D. W. Webb, malaise trap in tropical forest; 1 ♂, Mt. Koghis, 800 m, 1–6 Sept. 1972, J. F. McAlpine; 1 ♂, Mt. Dzu-

mac, 900 m, 166°28'E 22°1'45"S, 1–10 Nov. 1986, R. L. Brown, Malaise trap (DAVIS, ILLINOIS, OTTAWA). This species was collected in November.

Etymology.—*Eirone laniensis* is named after the collection site in the La Ni Valley.

Discussion.—*Eirone laniensis* most closely resembles *koghisica* as discussed under that species. Additional diagnostic features include the presence of a midcoxal spine, apically convex clypeal margin and well-developed mesopleural lamella. Specimens from Mt. Koghis and Mt. Dzumac tend to be darker, with more black coloration than the rest. However, structurally they appear to be the same as the rest of the paratypes.

***Eirone maigretae* Baptiste, new species**
(Figs. 4, 10, 21, 27)

Male.—Body length 18–21 mm; forewing length 14–16 mm; face (Fig. 4) punctures tiny between antennal lobes and inner eye margins, contiguous to 0.5 PD apart, becoming slightly larger and less dense, 0.5–1.0 PD apart on frons and vertex; clypeus medially gently convex, apical truncation 2.2–2.3 MOD wide, punctures small and 0.5–1.0 PD apart medially; F-I 2.2×; F-II length 3.2× breadth; pronotal punctures tiny and 2–4 PD apart; scutal punctures tiny and nearly contiguous laterally, becoming 0.5–2 PD apart laterally; mesopleural punctures 0.5–2.0 PD apart; mesopleural lamella apically rounded and flat against body; scutellum punctate medially and submedially, punctures 1–2 PD apart; propodeum finely and densely shagreened, punctures 1–2 PD apart, impunctate laterally; abdominal segments finely shagreened, punctures tiny and 4–6 PD apart; metasomal sternum I with medial longitudinal keel extending about halfway from anterior edge, sloping obliquely to posterior margin; epipygium strongly convex in profile, apex rounded (Fig. 21); hypopygium with broadly rounded apex; genital capsule (Fig. 27): gonocoxa with at most an obsolescent ridge on inner sur-

face; aedeagus apical column elongate, sinuous, and slender, bending ventrally; penis valve with large, slender dorsal hook and ventral lobe strongly expanded apically; volsella dorsally large and fist-like with small subsidiary lobe with 3–5 long apical setae, ventrally with curved digitate lobe margined by erect, long, somewhat curly setae, apical margin with short erect setae. Head yellow, with black markings, except orange on pedicel, ventral surface of scape and apical rim of clypeus, on frons back to occiput, diagonal bands extending from upper posterior eye margins to occiput, flagellomeres and dorsal surface of scape, mandibular apex; pronotum yellow, with black markings anteriorly, submedially behind anterior carina to lateral area, posterior margin transparent and orange-tinted; mesopleuron orange, with black markings along upper anterior edge to wing fossa; scutum black, except anteromedially orange, with posterior submedial yellow longitudinal bands; scutellum black, with yellow submedially; metanotum black with yellow band medially; propodeum orange with black submedially, and medial longitudinal yellow band; legs orange, with black dorsally on the coxae, trochanters and femora; metasoma orange, with black on posterolateral area of T-I and on hypopygium; wing membrane brown, darkest apically, with dark brown-black veins; vestiture silvery to pale yellow on head and thorax, orange on metasoma.

Female.—Unknown.

Type material.—Holotype ♂: NEW CALEDONIA, trail to Mt. Panié, 22 km NW Hienghène, 11–25 Nov. 1992, D. W. Webb, E. & M. Schlinger, malaise trap, in tropical forest, 457 m (PARIS). Paratypes 28 ♂♂: 19 ♂♂, same data as holotype; 6 ♂, same as holotype, except, 11 Nov. 1992, E. & M. Schlinger, 238–548 m; 1 ♂, Mt. Koghis, 500 m, 17 km nne Nouméa, 3–4 Nov. 1992, M. E. Irwin, D. W. Webb, E. & M. Schlinger; 1 ♂, Mt. Koghis, 500 m, 17 km nne Nouméa, 24–26 Dec. 1991, M. E. Irwin, D. W.

Webb; 1 ♂, Mt. Panié, 250–350 m, 30 Oct. 1986, R. L. Brown, sweeping; (DAVIS, ILLINOIS, OTTAWA). This species was collected from late October into late December.

Etymology.—This species of *Eirone* is named after Carolyn S. Maigret.

Discussion.—*Eirone maigretae* can be distinguished from the other species lacking a midcoxal spine as discussed under *emarginata* and *webbi*.

***Eirone nasalis* Kimsey, new species**
(Figs. 7, 12, 28)

Male.—Body length 15–19 mm; forewing length 10–14 mm; face (Fig. 7) lower facial punctures tiny and nearly contiguous, except upper clypeal margin nearly impunctate; clypeus projecting subapically, with well-developed, horizontally oriented ventral bevel, apex medially forming anteriorly projecting knob, with long pale setae, strongly nasiform in profile; frons punctures larger and 0.5–1.0 PD apart, except nearly impunctate medially below midocellus; vertex punctures 0.5–1.0 PD apart; F-I length $2.7\times$ breadth; F-II length $2.8\times$ breadth; pronotal and scutal punctures 0.5–1.0 PD apart, becoming sparsest medially; mesopleural punctures 0.5 PD apart; scutellar punctures 1 PD apart laterally, becoming sparser medially; midcoxal spine present; propodeum primarily punctate, punctures 0.5–1.0 PD apart, except anterolaterally impunctate; abdominal segments finely shagreened, punctures irregularly spaced, 2–6 PD apart; metasomal sternum I with medial keel along entire length and abruptly declivous posteriorly (Fig. 12); epipygium with medial depression, apex bilobate, flattened in profile; hypopygium subrectangular, slightly narrowed and subtruncate apically; genital capsule (Fig. 28); gonocoxa with subapical ridge on inner surface and large subbasal lobe on dorsal margin connected to setose medial lobe on inner surface; aedeagus apical column elongate, extending more than two-thirds

length of gonocoxa, sharply angled ventrally, apex broadly elongate triangular; penis valve with slender and elongate dorsal hook and ventral lobe; volsella broadly truncate dorsally, ventral surface with row of erect curved setae. Black, with cream-colored or light yellow band along inner and outer eye margins; wing membrane light brown with brown veins; vestiture silvery on head, thorax and metasomal basal segments, black on apical segments.

Female.—Unknown.

Type material.—Holotype ♂: NEW CALEDONIA, trail to Mt. Panié, 22 km NW Hienghène, 11–25 Nov. 1992, D. W. Webb, E. & M. Schlinger, malaise trap in tropical forest, 600 m (PARIS). Paratypes 39 ♂♂, 25 ♂♂, same data as holotype, except 457 m; 6 ♂♂, same data as holotype, except 457 m and 11 Nov. 1992; 4 ♂♂, Mt. Mandjanié, 5.3 km wsw Pouébo, 9–26 Nov. 1992, D. W. Webb, 550 m, malaise trap in tropical forest (DAVIS, ILLINOIS). This species was collected in November.

Etymology.—The species name refers to the nose-like projection of the clypeus.

Discussion.—This species can be immediately recognized by the projecting nose-like clypeus. Additional diagnostic features include the large rounded mesopleural lamella, presence of a midcoxal spine and black body color.

***Eirone neocaledonica* Williams**
(Figs. 17, 29)

Eirone neocaledonica Williams 1945:415. Holotype ♂: New Caledonia: Thi River Valley near St. Louis (WASHINGTON), examined.

Male.—Body length 9–11 mm; forewing length 7–9 mm; face with tiny contiguous punctures between inner eye margins and antennal sockets; frons nearly impunctate, with punctures widely separated, particularly along medial sulcus; clypeus with punctures much larger than along inner eye margin, punctures 0.5–1.0 PD apart, but obscured by fine shagreening; clypeal apex narrowly truncate, truncation 2.2

MOD wide; F-I length $2.2\times$ breadth; F-II length $3\times$ breadth; pronotum almost impunctate with few scattered lateral punctures; mesopleural punctures 0.5–1.5 PD apart, with dense, fine shagreening between; mesopleural lamella rounded posteriorly; scutal punctures medially 3–5 PD apart, becoming finer and denser laterally, 1–2 PD apart; scutellum nearly impunctate medially, laterally punctures 1–2 PD apart, with dense, fine shagreening; propodeum laterally with large tubercle, nearly impunctate except small medial patch of punctures (2–5 PD apart) and laterally below tubercle punctures smaller and 0.5–1.0 PD apart; midcoxal spine present; metasomal sternum I strongly triangular in profile, sloping abruptly to posterior margin; epipygium convex with two large digitate apicolateral lobes; hypopygium flat and broadly angulate apically; genital capsule (Fig. 29): gonocoxa with medial swelling associated with tuft of long setae on inner surface; aedeagus apical column elongate, slender and sinuous, bending ventrally; penis valve with broad dorsal lobe and broad, wing-like apical lobe; volsella with broad dorsal lobe, setose medial lobe and asetose ventral surface; color: black; wing membrane untinted basally, brown-tinted apically, particularly in marginal cell of forewing; pubescence on head and thorax silvery, on metasoma black.

Material examined.—3 males (including the holotype): 9.1 km NW Sarraméa, Thi River Valley, and Mt. Koghis (17 km nne Nouméa) (HONOLULU, URBANA, WASHINGTON). This species was collected in the months of December and January.

Discussion.—*Eirone neocaledonica* is one of the most unusually modified species and does not resemble any other in the genus. It can be immediately recognized in the male by the bidigitate epipygium, tuberculate propodeum and mesopleuron and truncate clypeal apex.

Eirone nepouiensis Baptiste, new species
(Figs. 10, 13, 30)

Male.—Body length 10–14 mm; forewing length 9–11 mm; clypeal punctures discrete and nearly touching; clypeal apex bilobate in ventral view, apical bevel nearly horizontal in profile, apical truncation 2.8 MOD wide; punctures along lower inner eye margin tiny and contiguous; frons punctures much larger and 0.5–2 PD apart; vertex punctures 0.5–1.0 PD apart; F-I length 2.0 – $2.1\times$ breadth; F-II length 2.4 – $2.5\times$ breadth; pronotal punctation 1–4 PD apart, except nearly impunctate medially; scutal punctures 0.5 PD apart anteriorly and laterally, becoming 1–3 PD apart medially; scutellar punctures contiguous laterally, 2–3 PD apart medially; mesopleural punctation 1–3 PD apart, becoming much finer and denser near metapleural suture; propodeal punctures 1–2 PD apart, becoming impunctate sublaterally; metasomal punctures 2–4 PD apart; midcoxal spine present (Fig. 10); metasomal sternum I with medial carina extending one-third to one-half distance from anterior edge, obliquely sloping to posterior margin (Fig. 13); epipygium broadly rounded apically, medially depressed; hypopygium with bluntly rounded apex; genital capsule (Fig. 30): gonocoxa broad, inner surface without distinct ridges or lobes; aedeagus apical column slender, short, extending only slightly beyond penis valve; penis valve with broad, wing-like apical and basal lobes, dorsal lobe broadly rounded and hooked apically; volsella with bilobate and hooked dorsal surface, ventrally asetose and abbreviated; color black, with yellow markings on antennal lobes, clypeus except distal edge, inner and outer eye margins, basal two-thirds of mandibles, across anterior pronotal carina (broken medially) and near dorsolateral apex, pronotal lobe, basal edge of tegula, band submedially on scutum, spot on scutellum anterolaterally and posterolaterally, metanotum submedially

and at hind wing base attachment, mesopleuron with spot below tegula, forefemur anteriorly; propodeum posterolaterally; T-I-III with lateral spots; wing membrane brown, with dark brown veins; vestiture brownish on head and thorax, black on metasoma.

Female.—unknown.

Type material.—Holotype ♂ (right antennal flagellomeres 2–3 missing, flagellomeres IV–XI mounted on point below specimen): Presqu'île de Pindai, 6 km sw Népoui, 25 Dec. 1991, M. E. Irwin (PARIS). Paratypes, 2 ♂♂, Plage de Pindai, 6 km sw Népoui, 7–13 Nov. 1992, D. W. Webb, malaise trap in coastal dunes area (DAVIS, ILLINOIS). Specimens were collected in November.

Etymology.—This species is named after the collection site on Népoui.

Discussion.—The flattened metasomal sternum I, emarginate mesopleural lamella, midcoxal spine and black coloration are characteristics shared by *nepouiensis* and *transversa*. However, *nepouiensis* can be distinguished from *transversa* by the ventrally bilobate clypeus and nearly horizontal clypeal bevel.

Eirone nigra Brown

(Figs. 11, 31)

Eirone nigra Brown 1984:257. Holotype ♂: New Caledonia: Hienghène (HONOLULU), examined.

Male.—Body length 13 mm; forewing length 11 mm; face with tiny contiguous punctures between inner eye margins and antennal sockets; frons impunctate around medial sulcus, laterally punctures 0.5–1.0 PD apart; clypeus with punctures larger than along inner eye margin, punctures 0.5–1.0 PD apart; clypeus convex medially, apex narrowly truncate, truncation 1.2 MOD; F-I length twice breadth; F-II length 2.8× breadth; pronotal punctures 1–3 PD apart; mesopleural punctures 1–2 PD apart; mesopleural lamella short, apically emarginate; scutal punctures sparsest me-

dially (1–3 PD apart), becoming finer and denser laterally (0.5–1.0 PD apart); scutellum impunctate medially, denser laterally, lateral punctures 0.5–1.0 PD apart; propodeum punctate in small medial patch (punctures 1–2 PD apart) and laterally (punctures 0.5–1.0 PD apart), impunctate sublaterally; midcoxa without apical spine; metasomal sternum I gently convex, with short medial carina extending about half length, sloping gently to posterior margin; epipygium strongly convex, apically subtruncate; hypopygium flat, broadly rounded apically; genital capsule (Fig. 31): gonocoxa with swelling above volsella on inner surface; aedeagus with slender apical column bending ventrally; penis valve with long dorsal hook, ventral lobe with long slender digitate apical lobe bending dorsally; volsella with large, broadly rounded dorsal lobe, ventrally with densely setose digitate lobe; color: black, wing membrane dark brown-tinted, veins black; pubescence on head and thorax silvery, metasoma black.

Material examined.—Only the holotype has been seen. It was collected in Hienghène in January.

Discussion.—The lack of a midcoxal spine and short mesopleural lamella suggests a close relationship between *nigra*, and *maigretae* and *emarginata*. However, the shorter F-I, clypeal truncation narrower than the transantennal distance and the black abdominal setae distinguish *nigra* from these two species.

Eirone obtusidens Turner

(Figs. 5, 32)

Eirone obtusidens Turner 1919:236. Holotype ♂: New Caledonia: Noumea (LONDON), examined.

Eirone obtusidens var. *superstes* Cockerell 1929: 239. Holotype ♂: New Caledonia: Bourail (WASHINGTON). Synonymized by Brown 1984.

Male.—Body length 13–14 mm; forewing length 11–12 mm; face with tiny contiguous punctures between inner eye mar-

gins and antennal sockets; frons with punctures 0.5–2 apart, except impunctate along medial sulcus and adjacent to antennal socket; clypeus with punctures larger than along inner eye margin, punctures contiguous; clypeal apex broadly triangular, with single apicomedial lobe; F-I length $2.4\text{--}2.5\times$ breadth; F-II length $3.0\text{--}3.2\times$ breadth; pronotal punctures 1–3 PD apart; mesopleural punctures 1–2 PD apart separated by dense, fine shagreening; mesopleural lamella posteriorly rounded; scutal punctures densest along notauli (nearly contiguous), medially sparsest (0.5–1 PD apart); scutellum nearly impunctate medially, punctures denser laterally, 0.5–1.0 PD apart; propodeum punctate medially and propodeum punctate medially and laterally, 0.5–1.0 PD apart; propodeum punctate medially and laterally, punctures 0.5–1.0 PD apart, impunctate sublaterally; metasomal sternum I sharply keeled, keel somewhat hooked posteriorly, abruptly declivous posteriorly; epipygium and hypopygium flattened and apex narrowly subtruncate; genital capsule (Fig. 32): gonocoxa with low medial angular lobe on inner surface; aedeagus elongate, apical column broad and flattened, bending dorsally, apically truncate, column extending more than half its length beyond penis valve; penis valve with short dorsal hook, large, rounded ventral lobe and elongate basal lobe; volsella with bilobate dorsal projection, apical lobe capitate and ventral surface slender with row of long setae.

Material examined.—7 ♂♂ (including the holotype of *obtusidens*), from Prov. Sud, 7.5 km NW and 1 km NW Sarraméa, Rivière Bleue, Mt. Panié, Noumea and Bourail. Specimens were collected in October, November and January.

Discussion.—The shape of the clypeus in *obtusidens* and *anone* is unique among the New Caledonian species. *Eirone obtusidens* can be distinguished from *anone* by the gently convex metasomal sternum I as discussed under that species.

Eirone paniensis Kimsey, new species
(Fig. 6, 33)

Male.—Body length 7–12 mm; forewing length 6–10 mm; face (Fig. 6) punctation; clypeus shagreened, most punctures 1–2 PD apart, becoming sparser apically, inner eye margins with tiny, nearly contiguous punctures; frons with punctures 2–5 PD apart, impunctate medially; clypeus gently convex, apex broadly truncate, truncation 2 MOD wide; vertex punctures 2–5 PD apart; F-I length $2\times$ breadth; F-II length $3\times$ breadth; malar lobe subtending mandibular articulation tooth-like; pronotum impunctate and polished dorsally, side with punctures 1–2 PD apart; mesopleuron bulging and knob-like medially, punctures 0.5–2 PD apart, densest dorsally, mesopleural lamella broadly rounded apically and bending slightly ventrally; scutum strongly depressed posteriorly along notalices, finely shagreened, scutal punctures 0.5–5 PD apart, becoming nearly impunctate posteromedially; scutellar punctures 1–5 PD apart, nearly impunctate medially; propodeum finely shagreened and impunctate dorsally except for punctate medial band, strongly tuberculate sublaterally, becoming densely punctate laterally, punctures 0.5–2 PD apart; midcoxa with acute spine; metasomal sternum I broadly triangular in profile, sloping obliquely toward posterior margin, not medially carinate; epipygium broadly rounded apically, apical margin with slight medial indentation, convex in profile; hypopygium broadly rounded and spinose, with flattened apex; genital capsule (Fig. 33): gonocoxal inner surface smooth; aedeagus apical column slender, elongate and sinuous, extending more than two-thirds length of gonocoxa; penis valve with rounded dorsal and ventral lobes; volsella with large truncate and setose dorsal lobe, ventral surface with erect, dense row of setae. Body black, with pale yellow or cream-colored markings on mandibular base, lower half of clypeus,

along inner and outer eye margins, on antennal lobes, transverse band (broken medially and sublaterally) along anterior pronotal carina, spot on pronotal lobe, distal forecoxal spot and subalar spot on mesopleuron, spot on tegula and on scutellum laterally; wing membrane brown, becoming darkest on apical third, with black veins; vestiture silvery on head and thorax, black on metasoma.

Female.—Unknown.

Type material.—Holotype ♂: trail to Mt. Panié, 22 km NW Hienghène, 11–25 Nov. 1992, 600 m, tropical forest, malaise trap, D. W. Webb and E. & M. Schlinger (PARIS). Paratypes, 5 ♂♂, same data as holotype (DAVIS, ILLINOIS). All specimens were collected in November.

Etymology.—*Eirone paniensis* is named after the collection site, Mt. Panié.

Discussion.—Much like *neocaledonica*, *paniensis* has a prominent knob on either side of the propodeum and very similar aedeagus and penis valve. Both species are relatively small-bodied, 7–10 mm long, and black, with few pale markings. However, *paniensis* can be distinguished from *neocaledonica* by the strongly tuberculate mesopleuron, gonocoxa with large interior brush of long setae, and tooth-like genal projection. In addition, *paniensis* has a midcoxal spine and well-developed mesopleural lamella

***Eirone rivierensis* Baptiste, new species**
(Figs. 15, 34)

Male.—Body length 8–14 mm; forewing length 9–12 mm; facial punctures 1–3 PD apart, except area between inner eye margin and antennal bases with tiny, nearly contiguous punctures, and narrow impunctate longitudinal band below midocellus; clypeus convex medially and apically truncate, apical truncation 2 MOD wide; F-I length 2× breadth; F-II length 3× breadth; pronotal punctures 1–3 PD apart; mesopleuron projecting medially, integument shagreened, with punctures 1–2 PD apart, becoming denser dorsally;

mesopleural lamella rounded apically and bending ventrally; scutum punctate and shagreened laterally, punctures 0.5–1 PD apart, becoming sparsely punctate medially with punctures 1–3 PD apart; scutellum laterally punctate, punctures 0.5–1 PD apart, medially polished and impunctate; propodeum finely shagreened, with punctures 1–2 PD apart, except laterally 0.5–1 PD apart, sublaterally impunctate; midcoxal spine present; metasomal sternum I broadly triangular in lateral view, sloping obliquely posteriorly (Fig. 15); epipygium narrowly rounded apically, flattened in profile; hypopygium with narrowly rounded apex, apical rim medially thickened and spinose; genital capsule (Fig. 34): gonocoxa with angulate ridge subapically on inner surface; aedeagus with apical column flattened and becoming broadly subtriangular apically; penis valve small with sharply hooked dorsal and ventral lobes, occupying half or less the distance across genital capsule; volsella dorsally fist-like, ventral half forming a long flat surface with row of dense, stout setae. Body black, with light yellow or cream-colored markings on clypeus above apical margin, along lower two-thirds of inner and outer eye margins, antennal lobes, band along pronotal transverse anterior carina (broken medially), band anterolaterally and posterior lobe of pronotum; wing membrane brown, with brown veins; vestiture silvery on head and thorax, metasomal terga I–VII with long, erect black setae along posterior margin that are densest on VII; sternum II–VI with long, erect black setae along posterior margin.

Female.—Unknown.

Type material.—Holotype ♂ (left antennal flagellomeres II–XIII missing): Rivière Bleue Prov. Pk., 19–20 Nov. 1992, 213 m, D. W. Webb & E. and M. Schlinger (PARIS). Paratypes 9 ♂♂, 1 ♂, Rivière Bleue Prov. Pk., km 25.8 Rivière Bleue road, 5–16 Nov. 1992, 213 m, D. W. Webb, E. & M. Schlinger; 1 ♂♂, *ibid.*, except, 30 Oct.–3 Nov., M. E. Irwin, D. W. Webb; 2 ♂♂,

ibid., except, km 19.6, 18–20 Nov. 1992, D. W. Webb; 2 ♂♂, ibid., except, km 21.9, 20–28 Nov. 1992, M. E. Irwin, D. W. Webb; 1 ♂, 30 km NW Yaté, 550 m, 27–28 December 1991, M. E. Irwin, D. W. Webb; 1 ♂, Rivière Bleue Prov. Pk., trail to upper Rivière Bleue, 5–16 Nov. 1992, 290 m, D. W. Webb; 1 ♂, Rivière Bleue Prov. Pk., trail to Vallée de Pourina, 19–28 Nov. 1992, 850 m, D. W. Webb; (DAVIS, ILLINOIS). This species was collected in November and December.

Etymology.—This species is named after the collection site in Rivière Bleue Province.

Discussion.—This species can be recognized by the primarily black coloration, without any reddish coloration, presence of a midcoxal spine, rounded mesopleural lamellae and truncate clypeal margin. *E. rivierensis* is most similar to *colorata* but can be separated by the dense black tuft of setae protruding from T-VI and VII. This tuft of setae is absent in *colorata*.

***Eirone salteri* Brown**
(Figs. 16, 18, 35)

Eirone salteri Brown 1984:250. Holotype ♂: New Caledonia: St. Louis "Val" (HONOLULU), examined.

Male.—Body length 12–14 mm; forewing length 10–12 mm; face with tiny, contiguous punctures between inner eye margins and antennal sockets; frons with punctures 0.5–1.0 apart, except nearly impunctate medially; clypeus subapically concave, apex narrowly produced into two lobes, 1.2–1.4 MOD apart, surface finely shagreened, punctures much larger than along inner eye margin, 0.5–1.0 PD apart; F-I length 2.2–2.3× breadth; F-II length 3.2–3.4× breadth; pronotal punctures 0.5–1.0 PD apart; mesopleural punctures 0.5–1.0 PD apart; mesopleural lamella short, apically truncate; scutal punctation medially 1–2 PD apart, becoming finer and denser laterally, 0.5–1.0 PD apart; scutellar medial punctures 2–4 PD

apart, laterally 1–2 PD apart; propodeum with oblique sublateral swelling, punctures medially 1–3 PD apart, laterally contiguous to 0.5 PD apart, impunctate sublaterally; midcoxa with short apical tooth; meso-, metathorax and propodeum finely and densely shagreened between punctures; metasomal sternum I with sharp, posteriorly hooked, medial keel, overhanging metasomal sternum II; epipygium strongly convex, apically narrowed and truncate; hypopygium flat, apically narrowed and bilobate; genital capsule (Fig. 35): gonocoxa inner surface smooth, without distinct ridges or lobes; aedeagus with apical column elongate, slender and sinuous, bending ventrally; penis valve large, dorsal lobe with blunt hook, ventral lobe large and wing-like, extending apically; volsella with long curly setae along apical surface, dorsally large and capitate, ventrally with large flat lobe tipped by two long setae; color black, with whitish markings on antennal lobes, inner and outer eye margins, mandible base, clypeus, transverse anterior pronotal margin, pronotum adjacent to tegula, mesopleuron below tegula, scutellum with two lateral spots; metanotum medially; legs orange; wing veins orange, except stigma black; wing membrane dark yellow-tinted, apex often browner; vestiture on head and thorax silvery to yellowish, on metanotum brown to black.

Material examined.—4 ♂♂ (including holotype): Sarraméa, St. Louis Val, and 1 km n and 9.1 km NW Sarraméa. All specimens were collected in late December, January and February (DAVIS, HONOLULU, URBANA).

Discussion.—Diagnostic features of *salteri* include the presence of a midcoxal spine, mesopleural lamella short and sharply emarginate, keel-like metasomal sternum I overhanging metasomal sternum II, apically bilobate clypeus, bilobate epipygium and amber-colored wing membrane. Metasomal sternum I is the same odd shape as seen in *irwini*, but the other

features given above will immediately separate the two.

***Eirone subtuberculata* Brown**
(Fig. 36)

Eirone subtuberculata Brown 1984:253. Holotype ♂: New Caledonia: Mts. de Koghis (HONOLULU), examined.

Male.—Body length 15–17 mm; forewing length 11–14 mm; face with tiny contiguous punctures between inner eye margins and antennal sockets; frons with punctures contiguous to 0.5 PD apart, except impunctate along medial sulcus; clypeus produced into subapical knob, with punctures larger than along inner eye margin, punctures contiguous and shagreened; clypeal apex truncate, truncation 3.0–3.2 MOD across; F-I length 2.2–2.3× breadth; F-II length 3× breadth; pronotal punctures 1–3 PD apart; mesopleural punctures 0.5–1.0 PD apart, shagreened between punctures; mesopleural lamella posteriorly triangular to rounded; scutal punctures medially 0.5–1.0 PD apart, becoming finer and denser laterally, contiguous to 0.5 PD apart; scutellar punctures 2–3 PD apart, laterally 0.5–1.0 PD apart; propodeum punctures 1–2 PD apart except anterolaterally, impunctate and finely shagreened; midcoxa with short apical tooth; metasomal sternum I strongly produced into slightly hooked keel, sloping vertically to sternum II; epipygium flattened, apically broadly bilobate; hypopygium flat, broadly truncate apically, with slight medial emargination; genital capsule (Fig. 36): gonocoxa with large submedial swelling on inner surface and subbasal lobe on ventral margin; aedeagus apical column elongate, about two-thirds as long as gonocoxa, apically curved, expanded and lanceolate; penis valve with slender dorsal and ventral, apically hooked lobes, barely obscuring aedeagal base; volsella with broad dorsal lobe and slender obsolescent ventral surface, with short erect setae along apical margin; color

black, with occasional small faint pale mark on inner and outer eye margin; wing membrane brown-tinted, veins black; vestiture of head and thorax silvery, metasomal brown to black.

Material studied.—13 ♂♂: Mt. Koghis; 17 km nne Nouméa (DAVIS, URBANA, HONOLULU). All specimens were collected in the months of December, January and February.

Discussion.—*Eirone subtuberculata* appears to be most similar to *rivierensis* and *colorata* based on the presence of a midcoxal spine, emarginate mesopleural lamella, apically truncate epipygium and thin clypeal apical margin. However, it is much larger than these two species, ranging from 12–16 mm long. The metasomal sternum I of *subtuberculata* differs as well resembling that of *nasalis* with an abruptly declivous posterior margin.

***Eirone transversa* Brown**
(Fig. 37)

Eirone transversa Brown 1984:254. Holotype ♂: New Caledonia: Mts. de Koghis (HONOLULU), examined.

Male.—Body length 10–15 mm; forewing length 8–12 mm; face with tiny contiguous punctures between inner eye margins and antennal sockets; frons with punctures 1–2 PD apart, except impunctate along medial sulcus; clypeus slightly convex, with transverse subapical bevel, punctures larger than along inner eye margin, 0.5–1.0 PD apart, shagreened between; clypeal apex truncate, truncation 2.0–2.2 MOD wide; F-I length 2.1–2.2× breadth; F-II length 2.5–2.6× breadth; pronotal punctures tiny, 1–4 PD apart; mesopleural punctures 0.5–1.0 PD apart, finely shagreened between; mesopleural lamella short, apically emarginate; scutal punctures medially 1–2 PD apart, becoming finer and denser laterally along notauli, contiguous to 1 PD apart; scutellum nearly impunctate medially, lateral punctures 1–2 PD apart; propodeum punctate

medially and laterally, punctures 2–4 PD apart, impunctate anterolaterally and finely shagreened; midcoxa with apical spine; metasomal sternum I broadly convex, with short basal carina, sloping gradually to posterior margin; epipygium strongly convex, apex slightly bilobate or emarginate; hypopygium flat, with broadly rounded apex; genital capsule (Fig. 37): gonocoxa narrowed medially, inner surface relatively smooth without discrete ridges or lobes; aedeagus with slender and elongate apical column, reaching to apical third of gonocoxal, apical column medially arcuate, extending apically, not bending dorsally or ventrally; penis valve dorsal and ventral lobes broadly rounded without apical hook; volsella dorsally bilobate with long erect setae along apical margin, ventral surface with row of elongate erect setae; color black, with yellowish markings on antennal lobes, apical clypeal margin, mandibular base, spot on inner and outer eye margin, pronotum with medially broken transverse anterior band, pronotal angle adjacent to tegula, tegula, small anterolateral scutellar spot; wing membrane brown-tinted, veins black; pubescence of head and thorax silvery, metasoma black.

Female.—Body length 7–8 mm; body coarsely punctate, with fine, dense longitudinal striae; facial punctures large and somewhat striatiform; frons with obscure medial longitudinal groove; F-I as long as broad; F-II length $1.2\times$ breadth; clypeal apex truncate; pronotum rounded laterally; propodeum impunctate laterally, elongate with flattened dorsal surface and lateral edges rounded, not carinate; T-I continuous with II, not constricted posteriorly; metasomal sternum I with strongly projection medial keel, appearing sharply triangular in profile.

Material studied.—91 ♂♂, 1 ♀: Mt. Koghis; 17 km nne Nouméa; Rivière Bleue Prov. Pk., 9–10 km NW Sarraméa; 13 km se Kaala-Gomén; trail to Mt. Panié, 22 km NW Hienghène; Rivière Bleue Prov. Pk.

Rivière Bleue Road, km 21 and 26; Rivière Bleue Prov. Pk., 30 and 36 km NW Yaté; Rivière Bleue Prov. Pk., trail to Vallée de Pourina; Rivière Bleue Prov. Pk., trail to Upper Rivière Bleue (DAVIS, ILLINOIS). Specimens were collected in the months of October through January.

Discussion.—Most similar to *nepouiensis*, as discussed under that species, *transversa* can be distinguished from *nepouiensis* by the clypeal apex broadly rounded in ventral view and the apical clypeal bevel oblique when viewed in profile.

Eirone webbi Kimsey, new species (Figs. 8, 38)

Male.—Body length 8–13 mm; forewing length 7–11 mm; facial punctures tiny, contiguous to 1 PD apart across lower face, frons and vertex essentially impunctate and shiny; clypeus gently convex, apex narrowly truncate, truncation 2.1–2.3 MOD wide; F-I length $2\times$ breadth; F-II length $3\times$ breadth; pronotum highly polished and nearly impunctate, except laterally with scattered tiny punctures; mesopleural punctation consisting of small punctures about 1 PD apart, becoming nearly impunctate ventrally; mesopleural lamellae acute, strongly narrowed apically and bending somewhat ventrally (Fig. 8); scutum highly polished, punctures 2–8 PD apart; scutellum with punctures 1–5 PD apart, densest laterally; propodeum essentially impunctate, densely and finely shagreened; metasomal sternum I with short medial carina forming obtuse angle in profile; epipygium with narrowly rounded apex; hypopygium broadly rounded, with narrow, thickened spine-rimmed apical margin; genital capsule (Fig. 38): paramere with smooth inner surface; aedeagus with short apical column; penis valve with rounded dorsal lobe, ventral lobe short and apically hooked; volsella with large truncate dorsal lobe, setose medial lobe and ventral surface asetose. Body black, with pale yellow or cream-colored markings on mandibular bases, clypeus,

inner and outer eye margins, antennal lobe, pronotum with transverse band on anterior carina and narrow band on posterior lobe, mesopleuron with small subalar spot, tegula with small spot, scutellum with lateral spot, metanotum with medial spot, propodeum with postero-medial and small lateral spots (faint in holotype); wing membrane brown with black veins; vestiture sparse, silvery to yellowish on head and thorax, brown to black on metasoma.

Female.—Body length 5–6 mm; frons with medial longitudinal irregular groove extending two-thirds head length; head, thorax and abdomen covered with fine dense longitudinal striae; clypeal margin medially concave and broadly truncate; F-I length $1\times$ breadth; F-II length $1.3\times$ breadth; pronotum subquadrate, slightly narrowed anteriorly, dorsally impunctate except for irregular row of punctures extending medially and continuing across scutellum and propodeum; propodeum long and flattened, lateral edge rounded, not carinate, impunctate medially, with punctures clustered along margins; T-I nodose, strongly constricted posteriorly; metasomal sternum I shallowly convex, without distinct medial keel or carina; tergal punctures sparse and somewhat striatiform; T-VI with elevated longitudinal medial impunctate welt; body dark brown with pale setae.

Type material.—Holotype δ : NEW CALEDONIA, Rivière Bleue Prov. Pk., trail to Upper Rivière Bleue, 5–16 Nov 1992, 290 m, D. W. Webb, malaise trap across forest path (PARIS). Paratypes, 57 $\delta\delta$, 11 $\delta\delta$, same data as holotype; 2 $\delta\delta$, *ibid.*, except 3–5 Nov. 1992; 5 $\delta\delta$, *ibid.*, except 19–20 Dec. 1992; 1 δ , Rivière Bleue Prov. Pk., km 19.6 Rivière Bleue rd., 20–28 Nov. 1992, 183 m, D. W. Webb; 1 δ , Rivière Bleue Prov. Pk., km 25.8 Rivière Bleue rd., 17 Nov. 1992, 213 m, D. W. Webb, E & M. Schlinger; 1 δ , *ibid.*, except 19–20 Nov. 1992; 6 $\delta\delta$, Mt. Mandjanié, 5.3 km wsw Pouébo, 9–26 Nov 1992, D. W. Webb, 550

m, malaise trap in tropical forest; 2 $\delta\delta$, 1 δ , Rivière Bleue Prov. Pk., 30 km NW Yaté, 270 m, 27 Dec. 1991, M. E. Irwin, D. W. Webb; 1 δ , *ibid.*, except 36 km NW Yaté, 21 Dec. 1991, M. E. Irwin, D. W. Webb; 5 $\delta\delta$, Rivière Bleue Prov. Pk., trail to Vallée de Pourina, 19–28 Nov. 1992, 850 m, D. W. Webb; 19 $\delta\delta$, 1 δ , trail to Mt. Panié, 22 km NW Hienghène, 11–25 Nov. 1992, D. W. Webb, E. & M. Schlinger; 1 δ , same as previous location, except 11 Nov. 1992; 1 δ , Mt. Do, 14 km ne Bouloupari, 31 Oct.–4 Nov. 1992, M. E. Irwin, D. W. Webb, E. & M. Schlinger, 1000 m; 1 δ , Mt. Panié, 250–350 ft., 30 Oct. 1986, R. L. Brown; 1 δ , Rivière Bleue, 166°39.55'E 22°6'S, 18 Oct. 1986, R. L. Brown (DAVIS, ILLINOIS). Specimens were collected in the months of October and November.

Other material examined.—1 δ , Rivière Bleue Prov. Pk., trail to Vallée de Pourina, 19–28 Nov. 1992, 850 m, D. W. Webb; 1 δ , same as above, except trail to Upper Riv. Bleue, 16–19 Nov. 1992, 290 m.

Etymology.—This species is named after the collector, Donald W. Webb.

Discussion.—Most individuals of this species are entirely black. However, some are orange or have varying amounts of black and orange coloration. *Eirone webbi* is one of the New Caledonian species lacking a midcoxal spine, the others being *impunctata*, *emarginata*, *nigra* and *maigretae*. Unlike these species, *webbi* can be distinguished by the strongly apically narrowed and flattened epipygium and hypopygium. The epipygium is slightly indented apicomediaally and not broadly rounded as in the other species. In *webbi* the clypeal apex is broadly truncate, and the truncation has blunt lateral corners. In *maigretae* and even more so in *emarginata*, the corners are acute, and in *emarginata* the clypeus is apicomediaally emarginate. The epipygium in *maigretae*, *nigra* and *emarginata* is strongly convex in profile, not flattened as it is in *webbi*. *Eirone maigretae* and *emarginata* are considerably larger than *webbi*, ranging between 18 and 22 mm in length.

Although color and body size vary considerably in *webbi*, this species can be distinguished by the acute and ventrally pointed mesopleural lamella. In the few individuals where the lamellae have been broken off the narrowed and flattened epipygium and hypopygium and configuration of the clypeus will prove diagnostic.

E. impunctata is another species of *Eirone* from New Caledonia that lacks a midcoxal spine. Although we have not been able to

see the type of *impunctata*, *webbi* appears to be a different species based on Brown's description and illustrations of *impunctata*. A few specimens of *webbi* are small, relatively impunctate, and are the ferruginous color mentioned by Brown in his description of *impunctata* (1984). However, Brown does not mention the peculiar mesopleural lamellae seen in *webbi* and his illustration of the face of *impunctata* indicates that the clypeal truncation is considerably narrower than that of *webbi*.

KEY TO MALES OF THE NEW CALEDONIAN *EIRONE* SPECIES

1. Midcoxa without apical spine or tooth on posterior angle (as in Figs. 8, 11) 2
- Midcoxa with apical spine or tooth on posterior angle (as in Figs. 9, 10) 6
2. Mesopleural lamella elongate, apically acute (Fig. 8) and bending ventrally; epipygium strongly narrowed apically and flattened in profile (as in Fig. 20) *webbi* Kimsey
- Mesopleural lamella foreshortened, apically emarginate (as in Fig. 10), not bending ventrally; epipygium broadly rounded or truncate apically and strongly convex in profile (as in Fig. 21) 3
3. Small, body length 8 mm or less *impunctata* Brown
- Larger, body longer than 8 mm 4
4. Flagellomere I barely twice as long as broad; metasomal setae blackish; clypeus strongly convex medially, apex narrowly truncate, truncation narrower than distance from the outer margin of one antennal socket to that of the other; wing membrane dark amber *nigra* Brown
- Flagellomere I more than twice as long as broad; metasomal setae pale, silvery to yellowish; clypeus flattened medially, apex broadly truncate, truncation as wide or wider than distance from the outer margin of one antennal socket to that of the other; wing membrane yellowish to light brown tinted 5
5. Body black; clypeus with lateral angles of apical truncation acute or dentate; hypopygium apically truncate *emarginata* Brown
- Body predominantly orange, with some black and yellow; clypeus with apical truncation broadly angulate laterally (Fig. 4); hypopygium apically broadly rounded *maigretae* Baptiste
6. Mesopleural lamella abbreviated and emarginate posteriorly 7
- Mesopleural lamella not abbreviated, rounded or acute posteriorly 9
7. Sternum I medially keeled, posterior margin pointed medially and extending over base of sternum II (Fig. 14); clypeal apex bilobate; hypopygium apically bilobate (Fig. 18) *salteri* Brown
- Sternum I flattened posteriorly (as in Fig. 13); clypeus broadly rounded in profile, with broad subrectangular apical bevel 8
8. Clypeal apex in ventral view bilobate, apical bevel nearly horizontal in profile *nepouiensis* Baptiste
- Clypeal apex in ventral view broadly rounded, apical bevel oblique in profile *transversa* Brown
9. Clypeus subapically bulging, with polished medial knob and subtriangular apical bevel, nasiform in profile (Fig. 7) *nasalis* Kimsey
- Clypeus subapically flattened or broadly rounded, apex truncate or medially lobate (as in Figs. 2–6) 10

10. Clypeal apex medially clearly convex or lobate (Figs. 2, 3, 5) 11
- Clypeal apex truncate, flat or concave (Figs. 4, 6) 15

11. Metasomal sternum I medially keeled, posterior margin pointed medially and extending over base of sternum II (Fig. 12 and as in Fig. 14); clypeus weakly trilobate *irwini* Baptiste
- Metasomal sternum I posteriorly flattened or arched, if arched then abruptly declivitous before base of sternum II, not overlapping II (as in Figs. 12, 13, 15); clypeus convex or trilobate (Figs. 2, 3), or unilobate (Fig. 5) 12

12. Clypeal apex medially unilobate (Fig. 5) 13
- Clypeal apex medially convex or trilobate 14

13. Metasomal sternum I strongly keeled and abruptly declivitous posteriorly (as in Fig. 12) *anone* Kimsey
- Metasomal sternum I gently convex medially gently sloping posteriorly to sternum II ... *obtusidens* Turner

14. Clypeal apex medially obtusely rounded and thin-edged, without bevel (Fig. 3), broadly convex in profile; epipygium apicomedialemarginate (Fig. 20) *laniensis* Baptiste
- Clypeal apex medially broadly trilobate and projecting anteriorly, with well-developed horizontal bevel seen in ventral view (Fig. 2); epipygium apicomedialemarginate or truncate *koghisica* Kimsey

15. Gena with tooth-like projection adjacent to mandibular condyle (Fig. 6); mesopleuron medially tuberculate; propodeum sublaterally tuberculate *paniensis* Kimsey
- Gena rounded or with small angle adjacent to mandibular condyle (as in Figs. 2, 3, 5); mesopleuron and propodeum not tuberculate (except propodeum in *neocaledonica*) 16

16. Epipygium terminating in long digitate apicolateral lobes, flattened medially (Fig. 17); propodeum sublaterally tuberculate *neocaledonica* Williams
- Epipygium apically truncate or rounded, without digitate lobes; propodeum evenly convex, not tuberculate 17

17. Sternum I strongly arched and abruptly declivitous before base of sternum II (as in Fig. 12); clypeus with polished subapical tubercle and polished and thickened apical margin *subtuberculata* Brown
- Sternum I broadly rounded or elevated medially and extending obliquely to posterior margin (as in Fig. 15); clypeus without subapical tubercle, with thin apical margin 18

18. Terga VI and VII with dense tufts of long dense setae; body color black *rivierensis* Baptiste
- Terga VI and VII without dense tufts of setae, setae long and scattered; color black to orange *colorata* Brown

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Review of the Species of *Deutereulophus* (Hymenoptera: Chalcidoidea: Eulophidae) of North America

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Abstract.—Although species of *Deutereulophus* (Hymenoptera: Chalcidoidea: Eulophidae) are known in America north of Mexico, none have been described. In this paper five **new species** are recognized: *D. arizonensis*, *D. floridensis*, *D. occularis*, *D. pecki*, and *D. smithi*, and a key is presented.

Ashmead (1904) described the genus *Eulophopteryx* and included two species, not realizing that the generic name was preoccupied (Möschler 1878). The name *Deutereulophus* was supplied by Schulz (1906) as a replacement for *Eulophopteryx*. Girault (1913) described the genus *Entedonomorpha* and Girault (1913, 1915, 1922, 1938) and Yoshimoto and Ishii (1965) later added several species from Australia and Guam to this genus which was synonymized with *Deutereulophus* by LaSalle and Schauff (1992). Although *Deutereulophus* occurs in North America (Schauff et al. 1997), no species from that region have been described and no keys or other information are available.

The majority of specimens used for this study are from the eastern U.S. due to two factors: 1) extensive malaise trapping by Dr. D. R. Smith in Maryland and Virginia and an extensive collecting effort along the eastern seaboard in the mid to late 1980s by a team of scientists from Canada, and 2) the author is one of the few scientists familiar with the genus and was able

to recognize specimens in these collections and organize them for study. It is difficult, if not impossible, for other researchers to sort material from collections, because of the lack of identification aids or illustrations to guide them. I have not personally been able to examine or sort through all collections and therefore, I have not been able to obtain specimens from many parts of North America. This is especially true for the west coast of the U.S. and Canada. Although western collections have not yielded specimens of *Deutereulophus* to date, it is likely that at least one or a few species occur along the west coast.

In this paper, I review the species from North America and provide names and a key for them.

Acronyms for museums are: (CNC) Canadian National Collection, Ottawa, Ontario, Canada; (USNM) National Museum of Natural History, Smithsonian Institution, Washington, D. C., USA; (BMNH) The Natural History Museum, London, UK. Terminology for morphology follows Gibson (1997). A diagram showing measurements of the head is given in Fig. 9.

KEY TO SPECIES OF *DEUTEREULOPHUS*

- 1) Legs beyond coxae yellow; scutellum smooth (Figs. 5, 8) 2
- Legs beyond coxae at least partly black or brown, scutellum with distinct alutaceous or reticulate sculpture (Figs. 1, 3) 4

- 2) First funicular segment equal in length to second (Fig. 14) *pecki*, n. sp.
 – First funicular segment distinctly longer than second (about $1.5 \times$ as long) (Fig. 13) 3
- 3) Thorax and head with distinct metallic green sheen, posterior margin of the gena on line with the posterior margin of eye; vertex rounded and area behind evenly sculptured
 *floridensis*, n. sp.
 – Thorax and head black, without metallic green coloration; posterior margin of eye projecting behind posterior margin of gena (Fig. 7); vertex with transverse carina just behind ocelli, area below carina with distinct sculpture medially, smooth laterally .. *ocularis*, n. sp.
- 4) Vertex with distinct transverse carina behind ocelli (Fig. 1), nearly smooth behind posterior ocelli *smithi*, n. sp.
 – Vertex rounded and without distinct median carina, mostly reticulate behind posterior ocelli with v-shaped smooth area medially (Fig. 2) *arizonensis*, n. sp.

Deutereulophus Schulz

Eulophopteryx Ashmead 1904: 341, 342, 374.

Types species *Eulophopteryx chapadae* Ashmead (original designation). Preoccupied by *Eulophopteryx* Möschler 1878: 684.

Deutereulophus Schulz 1906: 146. Replacement name for *Eulophopteryx* Ashmead 1904 (not *Eulophopteryx* Möschler, 1878).

Entedonomorpha Girault 1913: 261. Type species *Entedonomorpha tennysoni* Girault (original designation). Synonymy by LaSalle and Schauff 1992: 17.

Diagnosis.—Head concave behind (Fig. 1), often with a transverse carina on the vertex behind the ocelli and with the posterior eye margin contiguous with the back of the head such that there is no noticeable temple when viewed dorsally; eyes setose; clypeus delimited by sutures above and lateral to the mouth margin; pronotum semiglobose, and rounded anteriorly, without a transverse carina; notauli complete; scutellum with curving (sinuate) lateral grooves converging posteriorly and meeting medially (Figs. 3, 5); propodeum with a simple median carina diverging posteriorly and bounding a large open area at the nucha (Figs. 4, 6), laterally with at least a partial plical carina and with a transverse carina below the spiracle that defines the dorsal edge of an area which lies nearly perpendicular to the spiracular surface and that usually contains a group of setae below and medial to the callus setae; petiole with a forward projecting flange on dorsal and lateral

surface; hypopygium reaching about half length of metasoma; outer ovipositor plates visible and generally reticulate; female funicle 3-segmented and with first funicular segment usually pedunculate (Fig. 13), clava 3-segmented; male funicle 4-segmented and usually with at least first 2 funicles pedunculate (Fig. 14); stigmal vein well developed; postmarginal vein equal to or slightly longer than stigmal vein.

Discussion.—While no phylogenetic analysis of relationships within the Eulophinae has yet been published, several characters of the thorax (e.g. the lateral scutellar grooves, complete notauli, median propodeal carina) strongly suggest that *Deutereulophus* is closely related to a group of genera that includes *Hyssopus*, *Elachertus*, and *Diglyphomorphomyia* and several others. The shape of the pronotum is very similar to that found in *Hyssopus* and is a feature not shared by most of the other eulophid genera.

The pedunculate male antennae and the usually pedunculate first funicular segment of the females, however, argue for a close relationship to *Diglyphomorphomyia* (an Australian genus). The presence of a group of setae below the spiracle, which is apparently an extension of the usual line of callus setae, may be unique to this genus. I have not been able to examine all the types of Australian *Deutereulophus* so it is not possible to make a definitive statement about that character at this time. In

some species from the South Pacific region, the area below the callus contains only one or a few setae.

The forward projecting flange (Fig. 4) on the dorsal and lateral surface of the petiole is also a feature which I have not observed in other similar genera of eulophines and which seems to be constant within the species examined. Some species of *Hoplocrepis* have lateral flanges on the petiole, but no dorsal flange.

The posterior bifurcation of the median propodeal carina that forms a large open areola at the posterior median margin of the propodeum, and the presence of at least a short forward projecting lateral carina that originates from the anterior lateral margin of the areola (Figs. 4, 6) both seem to be unique to *Deutereulophus*. They are present in all species and may be the most reliable defining characteristic of the group. I have seen species of *Hoplocrepis* which have a somewhat similar condition in which the median propodeal carina ends posteriorly at the nucha but does not clearly bifurcate or enclose a cell or areola.

The presence of sinuate lateral grooves on the scutellum has been used in keys (e.g. Schauff et al. 1997) but this character, while stable for all North America species I have examined, is highly variable in other parts of the world and has been observed in a modified form in some Australian species of eulophids which I would not place in *Deutereulophus*. Recent authors seem to agree that this genus contains a natural group of related species, and I believe that the characters cited above reinforce that conclusion. Examination of specimens borrowed from museums in the Pacific basin indicate that numerous species exist in that region and that the center of diversity of *Deutereulophus* is probably the Australasian realm.

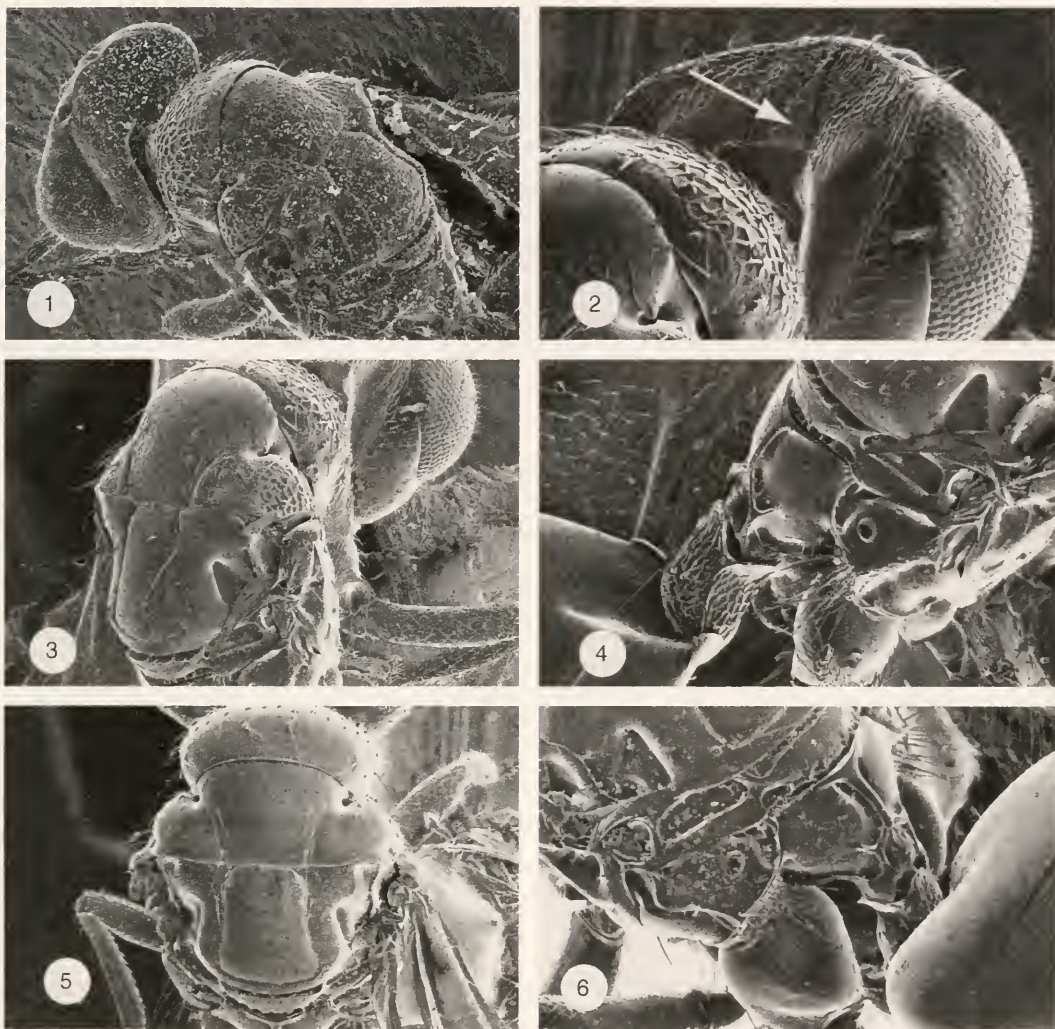
Deutereulophus arizonensis Schauff, new species
(Figs. 2, 3, 4)

Diagnosis.—Legs yellow except fore coxa black; funicles brown; vertex round-

ed, reticulate behind with inverted v-shaped smooth area (Fig. 2); mesoscutum and scutellum alutaceous (Fig. 3).

This species is similar to *D. smithi* but differs in that *smithi* has the vertex with a distinct transverse carina (Fig. 1), and the area behind the carina is lightly sculptured, nearly smooth, and without a distinct v-shaped area.

Description.—Female. Length 1.9 mm. Color black except: scape yellow, flagellum brown; fore coxa brown to black, rest of leg yellow. **Head**: Face lightly reticulate to nearly smooth, sculpture slightly heavier below toruli. In frontal view, head wider than high (40:35). Gena reticulate. Clypeus set off by irregular lateral and dorsal suture line. Mandible with one large ventral tooth and 3 smaller dorsal teeth. Malar suture complete, slightly curved. Ratio of malar space: eye height 10:32. Toruli inserted level with lower margin of eye. Ratio of width of face: width of eye 34:15. Occiput rounded, reticulate and with a central inverted v-shaped smooth area. Posterior margin of eye on same line as posterior margin of gena. Ocelli slightly removed from margin of occiput, POL 2× OOL. **Antenna**: Scape about 7× as long as wide. Ratio of length of F1:F2:F3:Clava 14:11:11:19, width 6 at F1 to 7 at clava. **Mesosoma**: (Fig. 3). Pronotum reticulate except at posterior margin, with numerous scattered setae. Mesoscutum smooth anteriorly, then becoming reticulate, with 2 pairs of setae along notaular margin, side lobes reticulate laterally, then alutaceous with a group of setae along anterior margin. Axilla smooth. Scutellum alutaceous to reticulate. Metanotum anteriorly projecting out from scutellum and bordered along median dorsal edge by a group of alveoli and by another band of finer alveoli along posterior margin. Propodeum medially smooth, with about 12 long white setae laterad of spiracle and about 20–25 setae below the spiracle. Petiole (Fig. 4) rugose dorsally, as long as wide, anterodorsal flange well developed, with



Figs. 1-6. Scanning electron micrographs of *Deutereulophus*. 1, *D. smithi*, thorax and head. 2, *D. arizonensis*, head, posterior view. 3, *D. arizonensis* thorax. 4, *D. arizonensis*, propodeum and petiole. 5, *D. floridensis* mesoma. 6, *D. floridensis* propodeum.

lateral flanges well developed. Forewing. Hyaline, $2.3\times$ as long as wide. Submarginal vein with 6-7 dorsal setae. Ratio of submarginal: marginal: stigmal: postmarginal vein = 33:33:12:15. **Metasoma:** Ovate, slightly longer than wide. Ovipositor sheaths reaching just past tip of gaster.

Male.—Unknown.

Distribution.—Known only from Arizona.

Types.—Holotype female with data: Ar-

izona, Patagonia, 27 June 1953. W. W. Wirth Collector. Deposited in USNM.

Etymology.—This species is named for the locality of the type.

Deutereulophus floridensis new species
(Figs. 5, 6, 12)

Diagnosis.—Head, lateral lobes of mesoscutum, and propodeum metallic green; in lateral view, posterior margin of eye not distinctly protruding behind hind margin

of gena; vertex rounded, without transverse carina and area behind uniformly smooth or lightly sculptured; mesoscutal midlobe and axilla smooth; scutellum smooth or very lightly alutaceous (Fig. 5); metasoma mostly yellow; legs white to yellow. Male scape with a small sensory patch containing only about 2 sensilla (Fig. 12).

This species is similar to *D. occularis*, which shares a smooth scutellum and yellow legs. However, *D. floridensis* has the thorax and head distinctly metallic green whereas *D. occularis* has a black head. *D. floridensis* has the posterior margin of the eye in lateral view not projected behind the gena and the vertex is rounded and uniformly sculptured behind (*occularis* with median transverse carina on vertex and the posterior margin of the eye projecting behind margin of gena (Fig. 7) and a distinctly sculptured area below occiput contrasting with the smooth lateral areas).

Description.—Female. Length 1.6–2.0 mm. Color: face, mesoscutal midlobe, axilla, and propodeum, occasionally lateral margin of metasoma metallic green; back of head, pronotum, scutellum, lateral thorax, ventral thorax, petiole black; antenna yellow except clava sometimes light brown; legs yellow to white; metasoma yellow except with brown on lateral margin and usually with an elongate triangular brown area medially on the posterodorsal surface. **Head:** Face and vertex smooth. In frontal view, wider than high (57:38). Gena reticulate. Clypeus set off by irregular suture line. Mandible with one large ventral tooth and 3 smaller dorsal teeth. Malar groove complete, slightly curved. Ratio of malar space: eye height = 8:13. Toruli inserted level with lower margin of eye. Ratio of width of face: width of eye = 31:15. Occiput rounded, area behind smooth to lightly alutaceous, shiny. Posterior margin of eye in lateral view on same line as posterior margin of gena. Ocelli contiguous with margin of occiput, POL 2× OOL. **Antenna:** Scape about 6×

as long as wide. Ratio of length of F1:F2:F3:Clava = 15:11:12:22, width 6 at F1 to 7 at clava. **Mesosoma:** Pronotum weakly alutaceous to smooth, with numerous scattered setae (Fig. 5). Mesoscutum smooth anteriorly, then becoming alutaceous posteriorly, with 2 pairs of setae along notaular margin, side lobes smooth, with group of setae along anterior margin. Axilla smooth. Scutellum very weakly alutaceous medially. Metanotum smooth, projecting out from scutellum anteriorly. Propodeum smooth medially, with about 10 long white setae lateral to spiracle and about 12–15 setae below the spiracle (Fig. 6). Petiole rugose dorsally, about as long as wide, anterodorsal flange small with lateral flanges well developed. Forewing. Hyaline, 2.3× as long as wide. Submarginal vein with 5–6 dorsal setae. Ratio submarginal: marginal: stigmal: postmarginal vein = 40:30:12:15. **Metasoma:** Ovate, slightly longer than wide. Ovipositor sheaths reaching just past tip of gaster.

Male.—Similar to the female except: Antenna with scape about 5× as long as wide. Flagellum with ratio of F1:F2:F3:F4: clava = 15:15:15:15:24. Scape with a very small sensory patch containing only 2 sensilla just above midline (Fig. 12).

Distribution.—Known only from Florida.

Types.—Holotype female with data: Florida: Monroe Co., No Name Key, 23.II–3.VI. 1986. S&J Peck, 86-13, hammock, FLT. Deposited in CNC. Paratypes: 1 female and 2 males with same data; 2 males with same data except 3.VIII–18.XI.1985, S&J Peck, hammock forest, malaise & FLT; 1 female and 1 male with same as previous except 4.V–4.VIII.1985; 5 females and 3 males same as holotype except Fat Deer Key, 18.XI.1985–25.II.1986, S&J Peck, hammock forest, malaise & flight intercept trap; 1 male with same data as previous except 2.VIII–16.XI.1985; 3 females and 5 males same as holotype except Big Pine Key, S1, T67S, R29E, 30.VII–17-XI.1985, S&J Peck, Cactus Hammock, malaise &



Figs. 7–8. Scanning electron micrographs of *Deutereulophus occularis*. 7, Head and anterior mesosoma, side view. 8, mesosoma, dorsal view.

flight intercept trap, forest; 1 female same as previous except 6.VIII–17.IX.1985; 1 female same as holotype except Everglades National Park, 1.5 km NW Royal Palm, 3.III.–28.IV.1985; 1 female same as holotype except N. Key Largo, Sec. 35, 1.VIII–16.XI.1985, S&J Peck, hammock forest, malaise & flight intercept trap; 1 female same as holotype except Sugar Loaf Key, Kitchings, 26.II–6.VI.1986, S&J Peck, 86–29, hammock forest FIT; 1 male same as previous except SE $\frac{1}{4}$, S23, 26.II–6.VI.1986, 86–31, hammock for., FLT, deposited in CNC; 1 female and 1 male same as previous deposited in USNM.

Etymology.—This species is named for the state locality of the type series, Florida.

***Deutereulophus occularis* Schauff, new species**

(Figs. 7, 8, 10)

Diagnosis.—Legs and antenna yellow; posterior margin of eye projecting behind posterior margin of gena (Fig. 7) in lateral view; vertex with transverse carina and area below distinctly sculptured medially contrasting with smooth lateral area; head and thorax black; mesocutum and axilla smooth. Male scape with sensory patch extending for most of top half of scape with about 13 sensillae (Fig. 10).

This species is somewhat similar to *Deutereulophus floridensis* which also has the dorsal thorax mostly smooth and shiny.

However, *D. floridensis* has a distinct metallic green sheen to the head (black in *occularis*), mesoscutal side lobes and propodeum, and the posterior margin of the gena is on line with the posterior margin of the eye. In addition, *D. floridensis* has the posterior margin of the eye ending about in line with the posterior margin of the gena when viewed laterally, and the vertex is rounded and not carinate.

Description.—Female. Length 2.3 mm. Color: Head and thorax black, antenna and legs light yellow except base of fore coxa brown; metasoma yellow except lateral margin of all but first tergum brown and with a median triangular brown spot which covers the last two terga and the median portion of the previous two terga. **Head:** Face and vertex mostly smooth with faint reticulation near eyes and on vertex. In frontal view, wider than high (56:38). Gena smooth. Clypeus set off by irregular suture line. Mandible with one large ventral tooth and 3 smaller dorsal teeth. Malar groove complete, slightly curved. Ratio of malar space: eye height = 10:25. Toruli inserted level with lower margin of eye. Ratio of width of face: width of eye = 28:15. Vertex with transverse carina, area behind carina smooth laterally and striate alutaceous to reticulate medially. Posterior margin of eye projecting behind posterior margin of gena (Fig. 7). Ocelli contiguous with margin of

vertex, POL $2.5\times$ OOL. **Antenna:** Scape about $6.5\times$ as long as wide. Flagellum with ratio F1:F2:F3:clava = 15:11:11:20, width 6 at F1 to 7 at clava. Scape with a sensory patch containing about 13 sensilla extending for almost entire length of top half (Fig. 10). **Mesosoma:** Pronotum weakly alutaceous to smooth, with numerous scattered setae (Fig. 8). Mesoscutum smooth anteriorly, then becoming alutaceous, with 2 pairs of setae along notaular margin, side lobes smooth, with a group of setae along anterior edge. Axillae smooth. Scutellum very weakly alutaceous medially. Metanotum projecting out from scutellum anteriorly, smooth. Propodeum smooth medially, with about 7 long white setae latera to spiracle and about 30 setae below spiracle. Petiole rugose dorsally, about as long as wide, dorsal anterior flange large and tongue-like with lateral flanges well developed. Forewing. Hyaline, $2.5\times$ longer than wide. Submarginal vein with 6–7 dorsal setae. Ratio submarginal: marginal: stigmal: postmarginal veins: 45:50:20:25. **Metasoma:** Ovale, slightly longer than wide. Ovipositor sheaths reaching just past tip of gaster.

Male.—Similar to the female except: Antenna with scape about $5\times$ as long as wide, with sensory patch about $\frac{1}{2}$ length of scape and containing 12–15 sensillae (Fig. 10). Flagellum with 4 funicular segments and 2-segmented clava. Ratio of F1:F2:F3:F4:clava = 15:15:15:15:24.

Distribution.—Known only from the type locality in Florida.

Types.—Holotype female with data: Florida: Monroe Co., NoName Key, 19-XI-85–25-II-86. S. & J. Peck. Hammock forest. Malaise & FIT. Deposited in CNC. Paratypes 1 female and 1 male with same data except female collected 3-VIII–18-XI-85 and male collected 4-III–29-IV-85. Female paratype deposited in USNM, male in CNC.

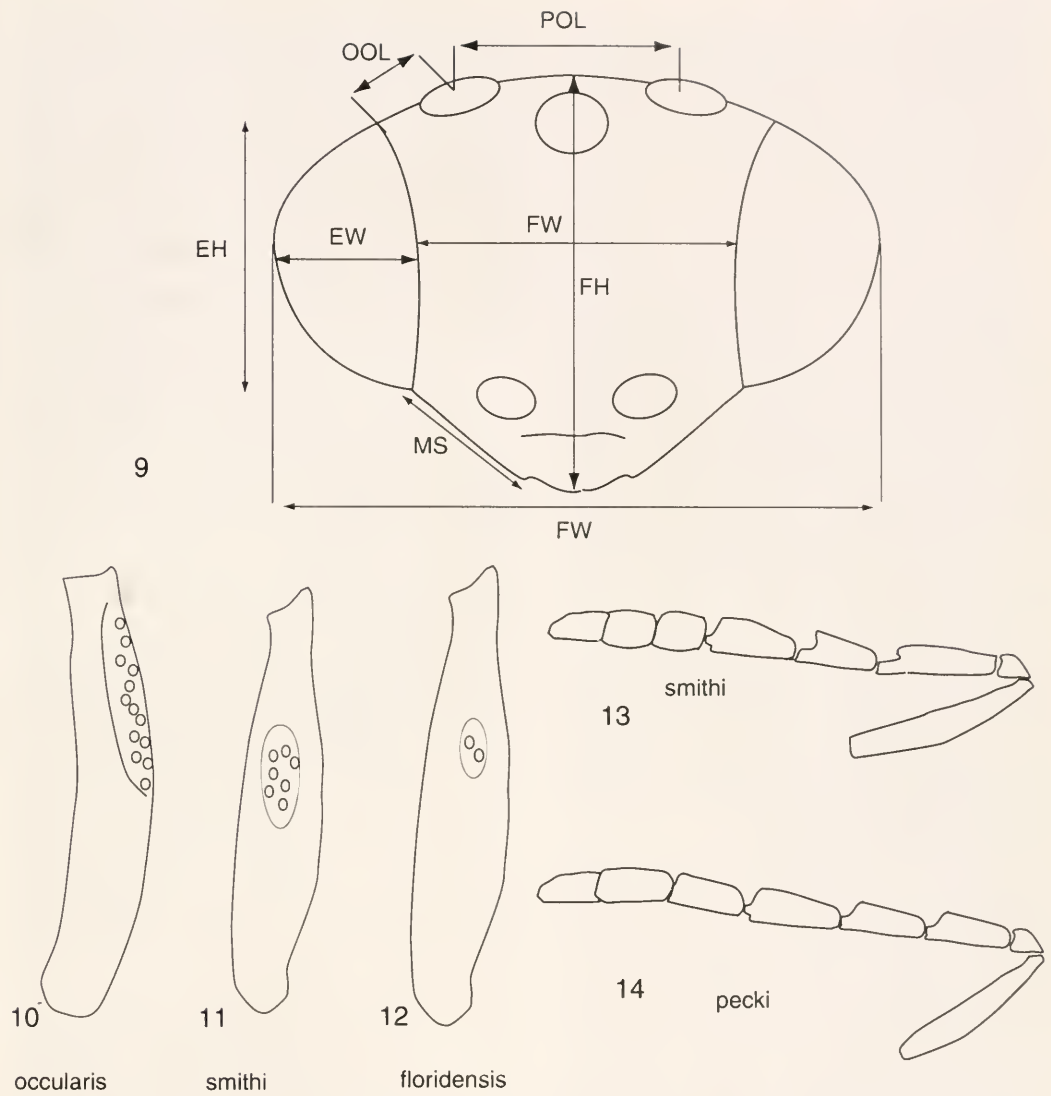
Etymology.—This species epithet refers to the eyes.

***Deutereulophus pecki* Schauff, new species**
(Fig. 14)

Diagnosis.—Legs yellow; antennal funicle brown; first funicular segment equal in length to second; mesoscutum, axilla, and scutellum mostly smooth with only very light reticulation on anterior mesoscutum.

This species is similar to *D. occularis* and *D. floridensis* in that the scutellum is smooth and the legs yellow. However, *D. pecki* has the first funicular segment of the female antenna equal in length to the second (distinctly longer in both *D. occularis* and *D. floridensis*) and the flagellum brown (yellow in *D. occularis* and *D. floridensis*).

Description.—Female. Length 1.1 mm. Color: Head and thorax dark brown; scape and legs light yellow; funicle brown; metasoma yellow. **Head:** Face and vertex mostly smooth with faint reticulation near eyes and on vertex. In frontal view, head wider than high (56:38). Gena smooth. Clypeus set off by irregular suture line. Mandible with one large ventral tooth and 3 smaller dorsal teeth. Malar suture complete, straight. Ratio of malar space: eye height = 12:25. Toruli inserted level with lower margin of eye. Ratio of width of face: width of eye = 33:15. Vertex acute, but without transverse carina, striate alutaceous to reticulate above and smooth below. Posterior margin of eye ending before posterior margin of gena. Ocelli slightly removed from margin of occiput, POL $2.0\times$ OOL. **Antenna:** Scape about $6.5\times$ longer than wide. Ratio of length of F1:F2:F3:clava = 10:10:11:24, width 6 at F1 to 7 at clava (Fig. 14). **Mesosoma:** Pronotum weakly alutaceous to smooth, with numerous scattered setae. Mesoscutum smooth anteriorly to very weakly reticulate at lateral margin, with 2 pairs of setae along notaular margin, side lobes smooth medially and weakly reticulate at lateral margin, with a single seta along anterior edge. Axilla smooth. Scutellum smooth



Figs. 9–14. *Deutereulophus*. 9, Generalized head, anterior view. OOL = ocellar ocular length. POL = posterior ocellar length. EH = eye height. EW = eye width. FW = face width. FH = face height. MS = malar space. HW = head width. 10–12, male scapes. Figs. 13–14. Antennae. 13, female. 14, male.

with only a faint hint of reticulation medially. Metanotum smooth, projecting out from scutellum anteriorly. Propodeum smooth medially, with about 7 long white setae lateral to spiracle and about 6 setae below spiracle. Petiole rugose dorsally, about as long as wide, and anterodorsal flange large and tongue-like with lateral flanges well developed. Forewing. Hyaline, 2.4× as long as wide. Submarginal

vein with 4 dorsal setae. Ratio submarginal: marginal: stigmal: postmarginal veins = 40:30:20:15. **Metasoma:** Ovate, slightly longer than wide. Ovipositor sheaths reaching just past tip of gaster.

Male.—Unknown.

Distribution.—Known only from the type locality in Florida.

Types.—Holotype female with data: Florida: Monroe Co., Key Largo, Sec. 35,

1-VIII-16-XI-85. S&J Peck. Hammock forest. Malaise & FLT. Deposited in CNC.

Etymology.—This species is named for Stuart Peck who collected many of the specimens included in this study.

Deutereulophus smithi Schauff, new species

(Figs. 1, 11, 13)

Diagnosis.—Legs except coxae white to yellow except fore coxae black; first funicular segment distinctly longer than second; occiput with distinct median carina, evenly, but very weakly sculptured, nearly smooth behind posterior ocelli; mesoscutal side lobes reticulate or alutaceous; scutellum alutaceous. Male scape with small sensory patch containing about 6 sensillae (Fig. 11).

This species is similar to *D. arizonensis*, which also has mostly yellow legs (except for the fore coxae). However, *D. arizonensis* has a rounded vertex without a distinct transverse carina and occiput with a triangular smooth spot bordered laterally by distinct sculpture (Fig. 2).

Description.—Female. Length 2.0–2.2 mm. Color black except as follows: scape white, pedicel and first funicular segment yellow, remainder of flagellum brown; fore coxa brown or brown basally, becoming yellow in apical half, rest of legs yellow to white with occasional brownish infuscation on fore femur. **Head**: Face weakly reticulate to nearly smooth, sculpture slightly stronger below toruli. Head in frontal view, wider than high (FH: FW = 60:43). Gena reticulate. Clypeus set off by irregular suture line. Mandible with one large ventral tooth and 3 smaller dorsal teeth. Malar suture complete, slightly curved. Ratio of malar space: eye height = 8:13. Toruli inserted level with lower margin of eye. Ratio of width of face: width of eye = 38:15. Vertex with distinct transverse carina, occiput smooth to weakly alutaceous, shiny. Posterior margin of eye on same line as posterior margin of gena. Ocelli contiguous with margin of occiput,

POL 2× OOL. **Antenna**: Scape about 7× as long as wide. Ratio of length of F1:F2:F3:clava = 20:14:15:25, width 6 at F1 to 7 at clava (Fig. 13). **Mesosoma**: Pronotum reticulate except at posterior margin, with numerous scattered setae (Fig. 1). Mesoscutum smooth anteriorly, then becoming alutaceous to reticulate posteriorly, with 2 pairs of setae along notaular margin, side lobes reticulate laterally, then alutaceous with a group of setae along anterior margin. Axilla smooth. Scutellum alutaceous to reticulate. Metanotum projecting out from scutellum anteriorly and bordered along median dorsal edge by a group of alveoli and by another band of finer alveoli along posterior margin. Propodeum medially smooth, with about 12 long white setae laterad of spiracle and about 20–25 setae below spiracle. Petiole rugose dorsally, slightly wider than long, anterodorsal flange small with lateral flanges well developed. Forewing. Hyaline or with very slight infuscation below marginal vein, 2.1× longer than wide. Submarginal vein with 6–7 dorsal setae. Ratio submarginal: marginal: stigmal: postmarginal vein = 35:35:12:15. **Metasoma**: Ovate, slightly longer than wide. Ovipositor sheaths reaching just past tip of gaster.

Male.—Similar to female except as follows: Fore coxae sometimes completely yellow; antenna with scape about 5× as long as wide and with a small sensory patch containing about 7 sensillae just above midline (Fig. 11). Flagellum with ratio of F1:F2:F3:F4:clava = 20:17:17:17:24.

Distribution.—Florida, Georgia, Louisiana, Maryland, Texas, and Virginia. Most records are from Maryland, Virginia, and Florida but this is no doubt due to extensive collecting in these areas. The range is almost certainly broader than indicated by the specimens available.

Variation.—The forewing of females may have a noticeably infusate brown area behind the marginal vein which extends to the hind margin of the wing. Col-

oration of the metasoma ranges from nearly entirely black to mostly yellow with some brown spots laterally. The fore coxa may be entirely yellow or have the basal half brown to black. In one specimen from Texas with a very darkly infuscated area on the forewing, the legs are also light brown. The flagellum varies from a dark honey yellow to brown but in most specimens the color is distinctly lighter on the first funicle.

Types.—Holotype female with data: Virginia: Essex Co., 1 mi. E. Dunnsville, 17-IX-10-X-1991, Malaise trap. D. R. Smith. Deposited in USNM. Paratypes: 3 females same as holotype; 3 females Virginia: Louisa Co., 4 mi. S Cuckoo, 12-27.V.1987, J. Klope & D. R. Smith, malaise trap; 1 female and 4 males with same as previous except 19.VIII-2.X.1987; 1 female and 1 male 16-31.VII. 1987; 1 male 25.VI-5.VII.1987; 2 males 3-24.IX.1987; 1 female VA: Page Co., Shenandoah Nat. Pk., 5-22.V.1987, 1300m, CNC [BRD] Hym. team, malaise trap in meadow; 1 male VA: Fairfax Co., near Annandale, 29.III-11.IV.1988, malaise trap, D.R. Smith; 1 male Maryland: Howard Co., Clarksville, 3.VIII.1986; 1 female same as previous except 13.VII.1986; 2 females Florida: Monroe Co., Big Pine Key, Watson's Hammock, 3.VI-27.VIII.1986, S&J Peck, malaise trap deposited in USNM; 1 female Texas: Jim Wells Co., 8 mi. W Ben Bolt La Copita Research Station, 20.V.1987, 87/006, J.B. Woolley deposited in TAMU; following all deposited in CNC: 4 females Maryland: Calvert Co., 6 km W Prince Frederick, 18-26.VIII.1986, Sharkey; same as previous except 3 females and 5 males 25.VIII.1986; 2 females and 1 male 7 km S Prince Frederick, 24.IX-14.XI.1987, Malaise trap, hardwood forest, CNC [BRD] Hym team; 3 males 4 mi. S Prince Frederick Co., 16.IV.-7.V.1987, L. Masner, Flight intercept trap; Calvert Co., 1 female Scientist's Cliffs, 7.VII. 1987, G. Gibson; 1 female Port Republic, VIII-IX.1986, Sharkey & Monroe; 1 female Chesapeake Bay Beach, 13.VI.1985,

L. Masner, s.s., plants in forest; 2 males Seneca, Potomac River trail Mouth of Seneca Creek.), 16.VI.1986, L. Masner, SS, undergrowth along old canal; 1 male Prince George's Co., Patuxent Research Station 21-29.VI.1986. D. Wahl, Malaise trap; 1 female Kentucky: Rowan Co., 24 km SW Morehead, Cave Run Lake, 14.V-20.VIII.1983, M. Kaulbars; 1 female and 1 male Georgia: Clarke Co., Lake Herrick, Oconee Forest Park., 11-12.VII.1987, L. Dumouchel; 1 male McIntosh Co., Sapelo Island, 9-21.IX.1987, live oak forest, CNC [BRD] team; 1 male 15.IX-16.XI.1987; Athens, 1 female 14.IX.1987, L. Masner; 1 female and 1 male Louisiana: Grant Parish, 28 km N Alexandria, Stuart Lake Campground, 19-21.V.1983, M. Kaulbars; 4 males Florida: Alachua Co., Gainesville, 1.V-20.VIII.1988, D. Wahl, flight intercept trap; 1 female same as previous except (AEI), 30.IV.1987, SS, L. Masner, 87/14; 1 male 10-20.II.1987, W. Mason; 1 female 8-14.IV.1987; 1 female 15-22.III.1987, Malaise trap, hardwood forest; 1 male American Entomological Institute, 9-17.IV.1986, G. Gibson, sweep; 3 females and 5 males Tallahassee, 18-23.V.1986, H. Howden, flight intercept trap; 3 females Monroe Co., Big Pine Key, Watson's Hammock, I.XI.84-3.III.1985, S&J Peck flight intercept trap; 1 female same as previous except 19.XI.1985-25.II.1986; 1 female 3.V-3.VIII.1985; 23.II-3.VI.1986; 1 female 3.VI-27.VIII.1986, hammock forest, Malaise trap/flight intercept trap, 86-10; 2 females Dade Co., S Miami, 7900 Swth St., Old Cutler Hammock, 21.II-1.VI.1986, flight intercept trap, S&J Peck, hammock; 1 female Chekika State Recreation Area, 50 km SW Miami, Grossman Hammock, 1.IX.1984-3.III.1986, S&J Peck, flight intercept trap; 1 male 3.III.-28.IV.1985; 2 females and 3 males Fat Deer Key, 4.III-28.IV.1985, S&J Peck, hammock forest, malaise & flight intercept trap; 4 females Monroe Co., Everglades National Park, Royal Palm Hammock; 1.XI-3.III.1985, S&J Peck, malaise; 2 females and 3 males

1.5 km NW Royal Palm, 3.III.–28.IV.1985, hardwood hammock forest, malaise-flight intercept trap; 2 females N. Key Largo, Sec. 35, 4.III.–4.VIII.1985, S&J Peck, hammock forest, malaise & flight intercept trap; 4 females and 1 male same as previous except 4.III.–28.IV.1985; 1 male 4.VIII.–16.XI.1985; 1 female St John's Co., Theodore Roosevelt Preserve, 13.X.1980, Masner & Bowen, 8029; 1 female Liberty Co., Torreya St. Pk, 7.X.1980, 8022, Masner & Bowen; 4 females and 4 males Texas: San Jacinto Co., 5 km S Coldspring Double Lake Campground, 22–24.V.1983, M. Kaulbars; 1 male Brazos Co., College Station, 1982, R. Wharton, M. Hrnir, pan trap.

Etymology.—This species is named in honor of David R. Smith, Systematic Entomology Laboratory, USDA, who collected part of the type series and whose collecting over the years has added greatly to the U.S. National Collection of Insects.

ACKNOWLEDGMENTS

I thank Dr. C. Burwell, Queensland Museum, Brisbane; Dr. S. Heydon, Bohart Museum, University of California, Davis; Dr. J. LaSalle, CABI Bioscience, UK; and Dr. J. Huber, Canadian Forestry Service and Canadian National Collection, Ottawa for the loan of specimens. Ms. Tami Carlow provided technical assistance and editorial support. Drs. S. Heydon, N. Vandenberg, and D. Smith provided useful comments on drafts of the manuscript.

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NOTE

The Presence of Antero-lateral Abdominal Glands in *Euderomphale* (Hymenoptera: Chalcidoidea: Eulophidae)

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Quicke *et al.* (1997) discussed the presence of antero-lateral abdominal glands (ALAGs) in the braconid subfamily Braconinae, and provided detailed anatomical descriptions of them. Virtually all braconines possess these glands, although they are not known in other braconid subfamilies. They are eversible, sac-like glandular invaginations of the unsclerotized lateral cuticle between the terga and sternum on the first and second metasomal (second and third abdominal) segments. ALAGs are present in both sexes, and produce an odoriferous secretion which is characteristic of braconine wasps.

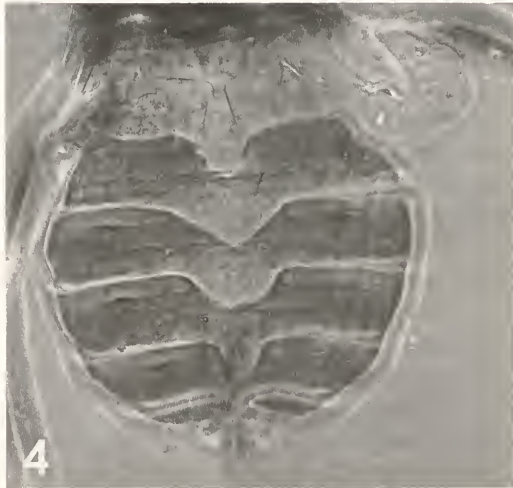
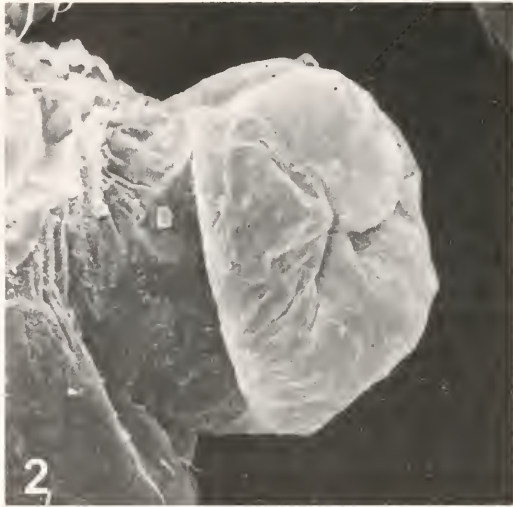
The exact function of ALAGs in braconines is unknown. Since the glands are everted, and their product secreted, most notably when the wasps are disturbed, Quicke *et al.* (1977) suggested that the product might be a chemical that was distasteful to predators. However, they also discussed several problems with this possibility, including that braconines were not distasteful to vertebrates, and that arthropods avoided non-braconines (without ALAGs) as readily as they avoided braconines (with ALAGs). Similarly, the role of ALAGs in the production of sex pheromones was questioned as these glands are present in both sexes. Another suggestion was that the ALAGs play a more general role in intra-specific signaling, such as an aggregation or alarm pheromone. Quicke *et al.* (1997) recorded ALAGs only in Braconinae and *Diprion*

similis (Diprionidae), although they concluded that it was unlikely that these are homologous structures.

The present paper reports the presence of ALAGs in the eulophid genus *Euderomphale*, species of which are parasitoids of whiteflies (see LaSalle and Schauff 1994 for a discussion of the systematic placement of this genus). This is the first report of the presence of these glands in any member of the Chalcidoidea.

The ALAGs in *Euderomphale* seem similar to those of braconines in that they appear to be eversible, sac-like invaginations of the unsclerotized cuticle between the terga and sternum of the second metasomal (third abdominal, first gastral) segment. There is only a single pair of the glands, and these are present in both sexes (Figs. 1–6). As with braconines, their function is unknown, but it is not clear that they are used in response to disturbance, as one of us (AP) has actually observed *Euderomphale* held in plastic bags everting and retracting these ALAGs while there was nothing obvious to disturb them. It may be that in *Euderomphale*, as suggested by Quicke *et al.* (1997), the ALAGs play a more general role in intra-specific signaling, but what this role might be remains unknown.

It is also worth noting that the shape of the anterior margin of the gastral tergites appears to provide useful characters for differentiation of species in *Euderomphale*. For example, in *E. cortinae* Graham (Figs.



3-4) the second gastral tergite is deeply emarginate medially, and there are similar emarginations on tergites 3 and 4, although these are more prominent in males (Fig. 4) than females (Fig. 3). In *E. flavimedia* (Howard) (Figs. 5-6), the first gastral tergite is slightly produced medially with a very small incision, with very broad, shallow lateral emarginations; tergites 3 and 4 are entire or only very slightly emarginate. This condition is found in

both males and females. Slide-mounted material is necessary to clearly see this character.

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Quicke, D.L.J., R.A. Wharton and H. Sittertz-Bhatkar. 1997. Antero-lateral abdominal scent glands of braconine wasps (Hymenoptera: Braconidae). *Journal of Hymenoptera Research* 6: 219-230.

←

Figs. 1-6. *Euderomphale* species. 1-4. *Euderomphale cortinae* Graham. 1, male gaster, showing ALAGs. 2, close up of ALAG. 3, female gaster. 4, male gaster. 5-6. *Euderomphale flavimedia* (Howard). 5, female gaster. 6, male gaster.

NOTE

First Possible Host Record for the Braconid Wasp Genus *Diamblomera* Enderlein (Hymenoptera: Braconinae)

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Determining host associations for parasitic wasps is fraught with difficulties and many published records are erroneous (Noyes 1994; Shaw 1994). These errors stem both from misidentifications of hosts and parasitoids, and from wrongly assuming associations. They are particularly problematic when it comes to concealed hosts, especially those living in deep or potentially complex situations where there may be more than one species, and the identity of the true host or hosts in these situations is often ambiguous.

Field observations in Sabah of a large braconine wasp, *Diamblomera* sp., strongly indicate that it is a parasitoid of larvae of cerambycid beetles belonging to the subfamily Lamiinae. Details of our observations and identifications are provided below.

During a reconnaissance visit to Poring Springs, a resort within lowland rainforest of Kinabalu National Park, Sabah, NML and DLJQ noticed a large female braconid wasp flying around a large dead (unidentified) tree. However, the wasp subsequently settled on a vine hanging from the tree and a second, apparently conspecific female wasp was then noticed already to be sitting on the same piece of vine about 20 cm away. Both wasps intermittently walked over that piece of vine, apparently searching for hosts, and after some time (approximately 5 minutes) one female raised her metasoma, 'located' her ovipos-

itor more or less between her hind legs and started 'drilling'. This activity was watched for approximately 15 minutes and as she then started moving her metasoma around more noticeably, it was thought that she may have located a host or even oviposited. At this point she was caught and the exact position where her ovipositor was 'drilling' was carefully noted. We proceeded to cut into this piece of dead vine. The stem of the vine is flattened and at this place was approximately 10 cm wide by 3.5 cm thick. Along a length of vine of approximately 40 cm we discovered more than twenty, apparently conspecific cerambycid beetle larvae belonging to the subfamily Lamiinae (identified as such because of the complete absence of legs, and the relatively elongate head with the cardines, submentum and maxillary articulating areas fused). These were almost all of very similar size (approximately 20 mm long, range 12–23 mm, and 2–3 mm wide) and apparently of an appropriate size to be a host for the wasp, *Diamblomera* sp., the females of which were approximately 18 mm long (excluding ovipositor), but a little narrower than the beetle larvae. No other potential hosts were present, i.e. no other even remotely similarly sized insect larvae were found. Unfortunately, no host was found immediately below the point of ovipositor penetration but since it took almost twenty

ty minutes for us fully to cut out and dissect this piece of vine, it is quite possible that any beetle larva had simply moved away from that place, possibly due to the disturbance we caused. A third individual of the wasp was subsequently observed flying around the site but she did not land on the now damaged vine. The vine was identified as *Agelaea borneensis* (Hook. F.) Merr. (Connaraceae) by Mr. Sukup Akin. *Agelaea* is a common SE Asian genus of trees, vines and shrubs (Jarvie and Ermayanti 1996 onwards).

Given that two females of the same species of *Diamblomera* were intensively investigating the same piece of host substrate with one starting to go through oviposition behaviour, and that the substrate contained many, apparently suitably sized larvae of a single species of cerambycid beetle, we feel confident that this is a valid host-parasitoid association. Unfortunately there are no identification keys to the species of *Diamblomera*. Only two species were described under that generic name originally (Enderlein 1920; Quicke and Achterberg 1990), and no further species have subsequently been transferred to it despite ongoing reclassificatory work; however, there probably exist other described species that are currently classified under different genera and full revision is needed.

This is the nearest thing to a first host record for a member of the genus *Diamblomera*, although it may be objected that none of the more than twenty putative hosts seen appeared to have been parasitised. The larger braconines belonging to the Aphrastobraconini (= Iphiaulacini) are often parasitic on concealed wood or stem boring hosts and this association with a vine-feeding cerambycid is therefore not exceptional, though records of parasitism of hosts in vines (lianas) are rare. Further, from what little is known about the hosts of the larger braconines (almost entirely from temperate taxa, particularly those associated with forestry pests), it appears that many attacking subcortical beetles may be quite polyphagous—but whether

all the host records that are listed in Shenefelt (1978) for members of such braconine genera as *Atanycolus* Foerster, which may have similar biologies to *Diamblomera*, are reliable is far from certain. That there is some degree of specialisation is apparent from the fact that, at the same locality, we observed several other species of large Braconinae—belonging to other genera—that were each showing interest in different sites or dead trees (Laurenne *et al.* 2000). Only the accumulation of accurate host records and other details of host ecology, such as substrate, plant or fungal associations, for these taxa will start to show what factors may be important in determining host ranges.

The specimens of *Diamblomera* and the beetle larvae are deposited in The Natural History Museum, London.

ACKNOWLEDGMENTS

We would like to thank Professor Maryati and Dr. Homathevi Rahman (TBCU, UMS, Sabah) for their assistance with planning this visit, Mr. Sukup Akin who kindly managed to identify the vine from a rather poor specimen, and Dr. Mark Shaw for valuable improvements to the MS.

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CORRECTION

P. S. Ward. On the identity of *Pheidole vaslitii* Pergande (Hymenoptera: Formicidae), a neglected ant from Baja California. *Journal of Hymenoptera Research* 9(1): 85–98.

Page 94, left column, line 30. The name "vaslilli" is incorrect and should be spelled *vaslitii*. This error was created at the proof stage by the editor, who regrets having added a further complication to the nomenclature surrounding this name.

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